

# Potential distribution of main malaria vector species in the endemic Colombian Pacific region

Yilmar Espinosa-Vélez<sup>1</sup>, Mariano Altamiranda-Saavedra<sup>1,2</sup> and Margarita M. Correa<sup>1</sup>

<sup>1</sup> Grupo de Microbiología Molecular, Escuela de Microbiología, Universidad de Antioquia, Medellín, Colombia

<sup>2</sup> Grupo de investigación en Comunidad de Aprendizaje Currículo y Didáctica, Politécnico Colombiano Jaime Isaza Cadavid, Medellín, Colombia

## Abstract

**OBJECTIVE** To assess the existing fundamental niche, potential distribution and degree of niche overlap for the three main Colombian malaria vectors *Anopheles albimanus*, *Anopheles darlingi* and *Anopheles nuneztovari* in the major malaria endemic Pacific region.

**METHODS** We used models based on presence records and Normalised Difference Vegetation Index (NDVI) data, created using the maximum entropy algorithm.

**RESULTS** The three vector species occupied heterogeneous environments, and their NDVI values differed. *Anopheles albimanus* had the largest niche amplitude and was distributed mainly on coastal areas. Environmentally suitable areas for *An. albimanus* and *An. nuneztovari* were the dry forest of inter-Andean Valleys in south-western Colombia, as confirmed for *An. albimanus* during model validation. There was a slight degree of niche overlap between *An. darlingi* and *An. nuneztovari*, and the species co-occurred in humid forests, predominantly in riparian zones of the San Juan and Atrato rivers.

**CONCLUSION** The information obtained may be used for the implementation of vector control interventions in selected priority areas to reduce malaria risk in this region while optimising resources.

**keywords** *Anopheles*, malaria, ecological niche modelling, Normalised Difference Vegetation Index – NDVI, Pacific region, Colombia, Niche overlap

**Sustainable Development Goals (SDGs):** SDG 3 (good health and well-being), SDG 15 (life on land)

## Introduction

Colombia ranks third in the number of malaria cases in Latin America [1]. In 2019, a total of 77 172 cases were reported and the Colombian Pacific region registered the highest number of cases in the country (44 804; 58.1%) [2]. Also in this region, the three Colombian main malaria vectors are present and were found naturally infected with *Plasmodium* parasites, *Anopheles* (*Nyssorhynchus*) *darlingi* with *Plasmodium falciparum* [3], *Anopheles* (*Nys.*) *nuneztovari* with *Plasmodium vivax* [4] and *Anopheles* (*Nys.*) *albimanus* with both parasite species [5].

*Anopheles* mosquitoes are distributed mainly in tropical and subtropical areas of the planet [6]. They are highly affected by climatic and environmental changes such as deforestation and urbanisation, which impact the quality and availability of water bodies used as their larval habitats [7]. Deforestation and changes in land use produce new environmental conditions that affect

mosquito species diversity [8] and may cause native species to be banished from the new environment [7]. In addition, climate changes may expand the altitudinal and latitudinal boundaries of mosquitoes [9]. Indeed, temperature variations influence larval and adult abundances; for example, a rise in environmental temperature accelerates development of the mosquito life cycle [10] and increases the frequency of blood intake and egg development [11]. Furthermore, precipitation can either increase the availability of larval habitats [12] or cause inundation of water bodies, reducing mosquito populations [13].

Ecological niche models (ENM) have been used to identify the environmental conditions that shape the geographic distribution of a species [14,15] and to estimate vector and disease dispersion patterns [15,16]. The niche of a species is estimated using georeferenced presence data and environmental variables as predictors, integrated into modelling algorithms to statistically calculate species distribution [17]. In the case of the malaria vectors, ENMs may help to improve vector control efforts for

malaria reduction [18,19]. In Colombia, among the few studies using ENMs for the main *Anopheles* vectors, one considered future scenarios of climate change and associated the geographic expansion of *An. albimanus* in northern Colombia with higher temperatures [20]. Another used Normalised Difference Vegetation Index (NDVI) data and determined that the rapid transformation of natural ecosystems would change the environmental conditions that define the potential geographic distributions of the three main malaria vectors, *An. albimanus*, *An. darlingi* and *An. nuneztovari*, in north-western Colombia.[14] Nonetheless, little is known about the environmental conditions that determine the presence and distribution of the main malaria vectors in the Colombian Pacific. This zone, in addition of being one of the most endemic regions in the country [21], presents diverse ecological and climatic conditions and among the highest levels of precipitation in the world [22]; moreover, human activities in the region that produce land use and landscape modifications are known to greatly affect the distribution and dispersal of malaria vectors [23]. Given this scenario, and also considering previous results on the potential geographic distribution of the three malaria vectors in the malaria endemic NW Colombian region [14], this work, based on the Grinnellian concept of the existing fundamental niche [15], tested the hypothesis that NDVI, used as the environmental variable and an indirect indicator of vegetation conditions, would allow to characterise the existing fundamental niche and the potential distributions of the three main malaria vectors, *An. albimanus*, *An. darlingi* and *An. nuneztovari* in the Colombian Pacific region. In addition, the degree of niche overlap or environmental similarity of the species niches was estimated. The information provided by the model and niche overlap is of relevance because it allows the selection of priority areas in the Pacific region for the implementation of efficient vector control interventions to reduce malaria risk.

## Materials and Methods

### Area of study, mosquito collection and occurrence data

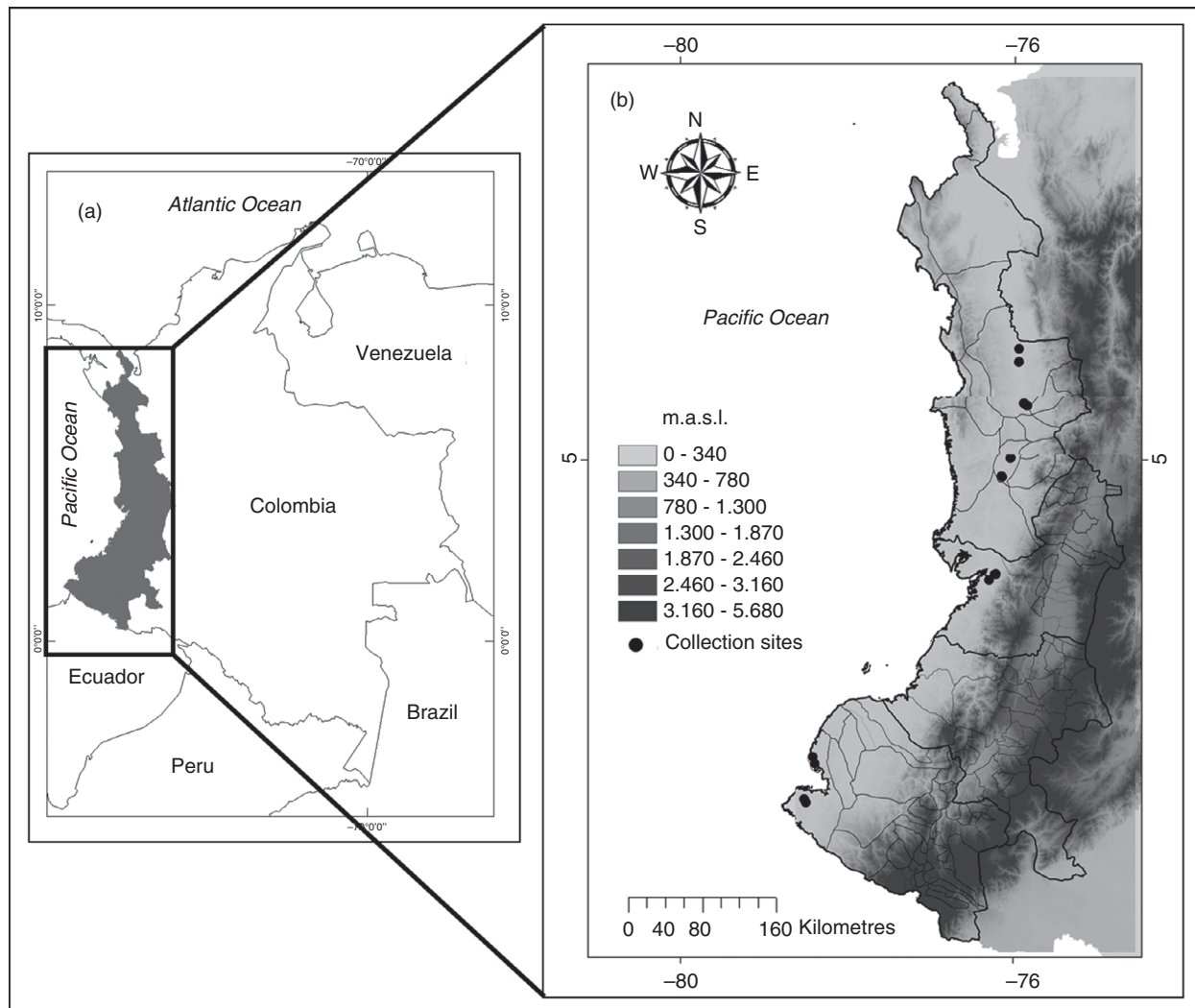
The Colombian Pacific region (Figure 1) in western Colombia includes the departments of Chocó, Valle del Cauca, Cauca and Nariño [22]. This region is part of the Chocó-Darién biogeographic province that extends from Panamá to the northern Ecuadorian border and is characterised by high species endemism [24]. Its subregions present diverse ecological and climate conditions; a tropical forest in the north, flooded plains, lakes and swamps in the coastal area, and a southern subregion characterised

by wetlands, mangroves and heterogeneous environments, most localities are heavily impacted by anthropic changes [4,22]. The altitude fluctuates between 0 and 1,800 m.a.s.l., the precipitation between 2,000 and 7,000 mm per year, and the average temperature is of 26°C [25,26]. All of these conditions are known to favour vector development and malaria transmission [21].

Mosquitoes were collected in eight municipalities of the Pacific region between March and November of 2015 (Table 1) using protected human bait, under a protocol approved by an institutional Bioethics Committee (Facultad Nacional de Salud Pública-UdeA, Acta 063). In each municipality, two localities were visited except in Buenaventura, where three localities were sampled. Collections were conducted for three nights, in six sites of each locality, by a team of four people, two people sampling one site each night, from 18:00 h to 24:00 h, both outdoors and indoors. The specimens were identified using a morphological key [27]. 25% of specimens and those presenting difficulties during species assignment were confirmed by PCR-RFLP of the internal transcribed Spacer 2 (ITS2), a DNA ribosomal region [28]. Data for each vector were organised as presence records in a database, with their coordinates in decimal degrees projected in the WGS84 system. To minimise problems of spatial autocorrelation because of proximity of some studied localities, and considering the heterogeneity and fine resolution of the NDVI environmental variable, a spatial filtering was performed. The aim was to eliminate redundant records considered to be grouped or very close within a distance, which, when incorporating the NDVI variable could present similar values [15]. In this study, most records for niche characterisation were collected in the field, which is a novel approach because they constitute high quality data. In addition, to increase the number of records, information from published articles was also included (Table 1).

### Environmental layers

To characterise the environmental space of the region, the Normalised Difference Vegetation Index (NDVI) was used. NDVI data are a product of the MODIS Terra satellite sensor, obtained in the form of satellite images at 250 m spatial resolution and 16-day temporal resolution [29]. The NDVI was used because it estimates vegetation photosynthetic capacity; it is a variable related to the climatic conditions that affect mosquito development [30], and it has the advantage of having fine spatial and temporal resolutions which allows characterising a greater environmental heterogeneity in the study area [14]. A total of 69 NDVI images were obtained for Colombia,



**Figure 1** Collection sites for *Anopheles albimanus*, *Anopheles darlingi* and *Anopheles nuneztovari* in the Colombian Pacific region. (a) Location of the Pacific region (in grey) in relation to Colombia. (b) Pacific region (dots represent the collection points).

encompassing the period January 2012–December 2014. Occurrence data from the following year to the NDVI data was used based on published information indicating that in the region during this period, deforestation occurred at very low rates [31]. NDVI values represent vegetation changes and seasonality [32], factors that influence aspects of mosquito biology such as development and species abundance. The images were subjected to a principal component analysis (PCA) with the aim of eliminating collinearity among images; the principal components (PCs) contain information on NDVI spatial and temporal variations [33]. From this analysis, the first 45 PCs that explained 95% of the cumulative variance were

selected and used as environmental layers for model calibration. The PCA analysis contributes to reduce accessory information; therefore, the selection of a high number of PCs does not cause overfitting [15].

#### Ecological niche models and potential distribution maps

To estimate the potential distribution of the three malaria vectors, ENMs were developed in MaxEnt 3.3.3k [34], which uses the maximum entropy algorithm [17]. This algorithm relates environmental conditions of the area with species presence and calculates the 'environmentally appropriate area' represented in a probability distribution

**Table 1** Mosquito collection data and literature records used to construct the models for *An. albimanus*, *An. darlingi* and *An. nuneztovari*

Department municipality	Locality	Collection dates	Species present (Number of records)	Longitude, latitude†
<b>Chocó</b>				
Atrato	El Arenal	18–20-Mar-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (5)	–76.643 5.551
	Doña Josefa	21–23-Mar-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (6)	–76.616 5.529
Medio Atrato	Tauchigadó	24–26-Mar-2015	<i>An. darlingi</i> (6)	–76.727 5.966
	Puné	27–29-Mar-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (2)	–76.728 6.088
Istmina	Basurú	3–5-Nov-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (6)	–76.790 4.979
	San Antonio	6–8-Nov-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (6)	–76.689 5.130
Medio San Juan	San Miguel	28–30-Oct-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (6)	–76.788 4.980
	Paimadó	31-Oct 2-Nov-2015	<i>An. darlingi</i> (6), <i>An. nuneztovari</i> (6)	–76.877 4.805
<b>Valle del Cauca</b>				
Buenaventura	La Barra	1–3-Sept-2015	<i>An. albimanus</i> (4)	–77.370 3.981
	Córdoba	10–12-May-2015	<i>An. nuneztovari</i> (6)	–76.930 3.871
	Zacarías	13–15-May-2015	<i>An. nuneztovari</i> (6)	–76.995 3.816
Dagua	Periurbano	4–6-May-2015	None	–76.686 3.656
	Juntas Dagua	7–9-May-2015	None	–76.687 3.655
<b>Nariño</b>				
Tumaco	Buchely	18–20-Ago-2015	<i>An. albimanus</i> (6)	–78.769 1.704
	Inguapi del Carmen	21–23-Ago-2015	<i>An. albimanus</i> (6)	–78.754 1.676
Francisco Pizarro	La Playa	24–26-Ago-2015	<i>An. albimanus</i> (5)	–78.641 2.043
	Salahondita	27–29-Ago-2015	<i>An. albimanus</i> (6)	–78.673 2.122
<b>Other studies (Source in brackets)</b>				
	Nuquí, Tumaco [28]*		<i>An. albimanus</i> (4)	
	Nuquí, Tumaco, Pizarro, Buenaventura [5]*		<i>An. albimanus</i> (7)	
	Tumaco, Buenaventura, Vigía del Fuerte [4]*		<i>An. albimanus</i> (2), <i>An. darlingi</i> (1), <i>An. nuneztovari</i> (2)	
	Tumaco, Salahonda Mosquera [58]*		<i>An. albimanus</i> (12)	
	Buenaventura [59]*		<i>An. nuneztovari</i> (1)	
	Buenaventura [60]*		<i>An. nuneztovari</i> (1)	
<b>Total records</b>			<i>An. albimanus</i> (52), <i>An. darlingi</i> (49), <i>An. nuneztovari</i> (53)	

[n]\*, source of records.

†Coordinates corresponding to localities where mosquitoes were collected in the Colombian Pacific region. The number of records in bold corresponds to georeferenced data used for model construction.

[34]. In MaxEnt, the models were calibrated entering five training sub-samples of each species and the principal components in sets of 5, 10, 15, 20, 25, 30, 35, 40 and 45 PCs. To avoid inconsistencies in model performance owed to differences in record sizes, the training and testing percentages varied among species. For *An. albimanus* (which had smallest records size), five training sub-samples were generated randomly using 80% of the records and five testing sub-samples with 20% of the remaining records. For *An. darlingi* and *An. nuneztovari*, five training sub-samples were generated with 90% of the records and the remaining 10% were used for sub-sample testing. Random sub-sampling was used with a sufficient percentage of presence data to minimise overfitting of models and to avoid redundant information during calibration [15]. By this method, several replicas of the model are

obtained allowing for the selection of those significantly better than any randomly generated model. To delimit the model accessibility area (M), in the initial approach, layers of the terrestrial ecoregions of the world [35] were used to determine for the Pacific region those that corresponded to the vectors' presence records. Altitude was used as the hypothesis of M for calibration of the models because it is a variable that is indirectly related to variables such as temperature [15]. Comparison of M for ecoregions with altitudinal distribution showed high concordance and a higher area of distribution; therefore, various altitudinal intervals were proposed based on the dispersion capacity of each vector [36]. For *An. albimanus* the intervals were 0–1800, 0–2000 and 0–2200 m.a.s.l. [37]; for *An. darlingi*, 0–1000, 0–1200 and 0–1400 m.a.s.l. [38], and for *An. nuneztovari* 0–1200, 0–

1400 and 0–1600 m.a.s.l. [39]. No clamping or extrapolation was permitted in MaxEnt, and the remaining parameters were left as default. Logistic output formats were used. ENMs were calibrated for each species with 10 bootstrapped replicates; the median across replicates was used as the basis for further analysis [38]. The uncertainty analysis was not performed.

For each vector and to assess model performance, the partial receiver operating characteristic (ROC) was tested according to the proportion of predicted areas, using the medians of the models and the five sub-samples, in NicheToolBox [40]. The partial ROC helped to decide what models performed better via the sensitivity (1 – omission rate) and the specificity (omission rate); models with values near 2 were considered [41]. Model selection was based on omission rate values equal or lower than zero. For each vector, the model with the best performance was selected and converted into binary-format maps (presence–absence). The conservative approach minimum training presence (MTP), fixed cumulative value (FCV) and 10 percentile training presence (10 PTP) reclassification thresholds were used to represent the appropriate areas for a species considering the lowest omission errors [42]. Reclassification showed the suitable (one) and unsuitable (zero) pixels for the vectors in the endemic area. To minimise uncertainty, the five maps from the sub-samples for each vector were combined into a single map that showed the sum of areas in common. Pixels with four and five values (80% and 100%, respectively) were selected to represent the final suitable area on the potential distribution map.

To understand the temporal and spatial behaviour of the vegetation in the Colombian Pacific region, loadings of the first two main components (PC1 and PC2) of each NDVI image were compared with the average monthly maximum precipitation values obtained for the period January 2012 to December 2014, from four hydro-meteorological stations selected based on their proximity to the localities of the study. PC1 loadings represented the condition and quality of the vegetation, whereas PC2 loadings explained the seasonal variation of NDVI with respect to precipitation [43]. PC1 and PC2 eigenvalues were used to compare vegetation characteristics of the available suitable and unsuitable environments. This methodological approach was used to compensate for the low interoperability in the biological meaning of PCAs.

### Niche overlap and model validation

For the three vectors, the minimum volume ellipsoid (MVE) was analysed in NicheA [44], using the three main PCs of the NDVI images and georeferenced

presence points. The Jaccard index (J) was used to quantitatively measure the degree of niche overlap between species pairs; this estimation allowed determining how many and which species can coexist in a community [45]. The niche superposition test was performed for species pairs in ENMTools, using the models predicted in MaxEnt [46]. The Schoener's *D* similarity metric was calculated for each pair of species [46,47]. The background similarity test was performed for each, comparing the random occurrence data from species 1 against the background of species 2 and in the opposite direction. Finally, a background similarity test was performed to compare the *D* metric and vector occurrence data, with a null distribution of 100 random replicates [47]. For each pair of species, histograms were plotted to show similarity results versus the *D* metric [46,47]. Subsequently, a map of the proportion of suitable and shared areas was constructed for the three vectors. Finally, to verify model predictive capacity, two localities situated within the predicted areas were visited and mosquito collections were performed for the vectors showing the widest geographic distribution.

## Results

### Ecological niche models and potential distribution maps

The records used to construct the models were 52 for *An. albimanus*, 49 for *An. darlingi* and 53 for *An. nuneztovari* (Table 1). The models obtained were significantly better than any randomly generated model ( $p > 0.001$ ) (Tables S1–S3). According to the Partial ROC and omission rate values, the highest performance models were, for *An. albimanus*, the 2200 m.a.s.l. altitude model with the first 40 PCs, for *An. darlingi*, the 1200 m.a.s.l. model and first 35 PCs and for *An. nuneztovari*, the 1600 m.a.s.l. model and first 45 PCs (Table 2). The MTP reclassification threshold helped to estimate suitable areas in the *An. albimanus* model (0.129, training omission  $<0.001$ ), while the FCV reclassification threshold was appropriate for estimating suitable areas in the *An. darlingi* and *An. nuneztovari* models (0.079 and 0.130, respectively, training omission  $<0.001$ ).

The *An. albimanus* distribution map showed wide geographic distribution for the species in the Pacific region, with suitable areas mainly on the coasts and lowlands, and specifically in subregions corresponding to the valleys of the Cauca and Patía rivers (35.625% suitable; Figure 2a). The environmental suitable areas for *An. darlingi* were municipalities along the Atrato and San Juan rivers in Chocó Department and Cali city in Valle del Cauca Department (3.780% suitable, Figure 2b). Suitable areas for *An. nuneztovari* were in the valleys of Atrato and San



**Table 2** Evaluation of the models selected for *Anopheles albimanus*, *Anopheles darlingi* and *Anopheles nuneztovari*

Species	Model*	PCs†	Partial ROC‡	Reclassification threshold	Predicted area	Omission rate
<i>An. albimanus</i>	2200 m.a.s.l.	40	1.991 (<0.001)	MTP	0.129	0
<i>An. darlingi</i>	1200 m.a.s.l.	35	1.999 (<0.001)	FCV	0.079	0
<i>An. nuneztovari</i>	1600 m.a.s.l.	45	1.999 (<0.001)	FCV	0.130	0

MTP, minimum training presence; FCV, fixed cumulative value.

\*The accessibility area (M) defined in metres above sea level (m.a.s.l.).

†Number of combinations of the main components (PC) that explains the consistency of the models.

‡In parentheses is the *p*-value of the partial ROC test.

Juan rivers including Quibdó city, in Chocó, the municipalities of Buenaventura and El Darién in Valle del Cauca and in the valleys of Cauca and the Patía rivers in Valle del Cauca and Cauca Departments (10.043% suitable, Figure 2c).

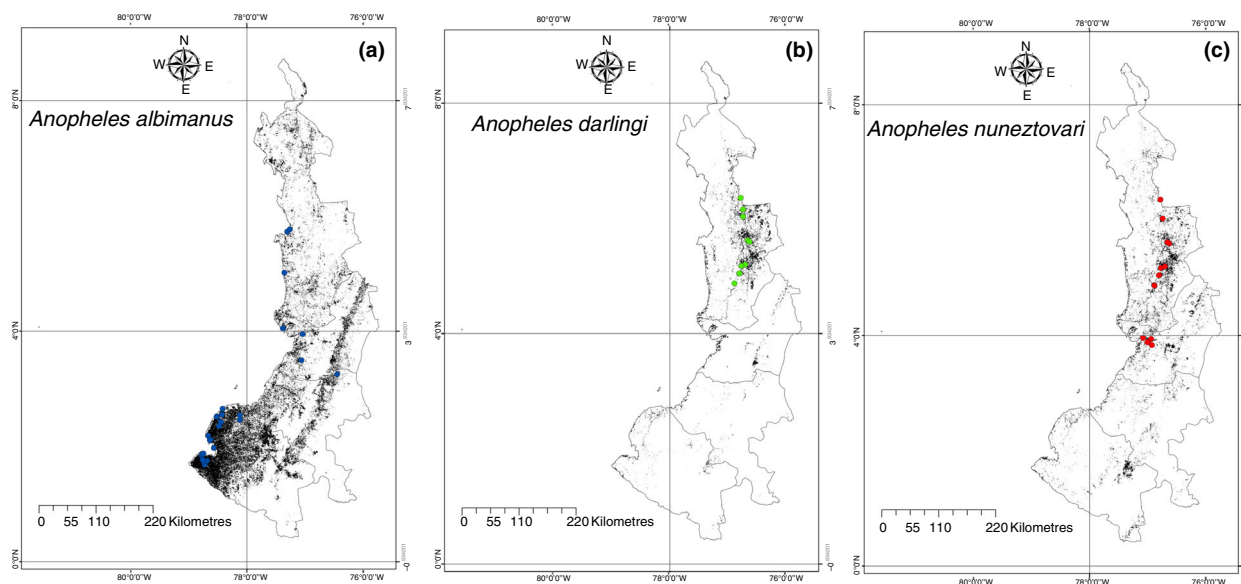
#### Relationship between vegetation and seasonality during the mosquito collection period

Regarding NDVI values, PC1 loadings showed a negative response for the entire period of NDVI images (Figure 3a), while PC2 loadings showed negative values in the seasons with the highest monthly precipitation and positive values in the months of lower rainfall (Figure 3b).

PC1 and PC2 explained 43.35% and 5.20% of the total variance, respectively. The environments occupied by the three vectors presented both positive and negative patterns in the NDVI eigenvalues. Unoccupied regions presented contrasting NDVI values. For example, some unoccupied environments showed stable NDVI eigenvalues associated with homogeneous and temporal stable environments, while other unoccupied locations presented NDVI eigenvalues varying over time (Figure 4).

#### Niche overlap and model validation

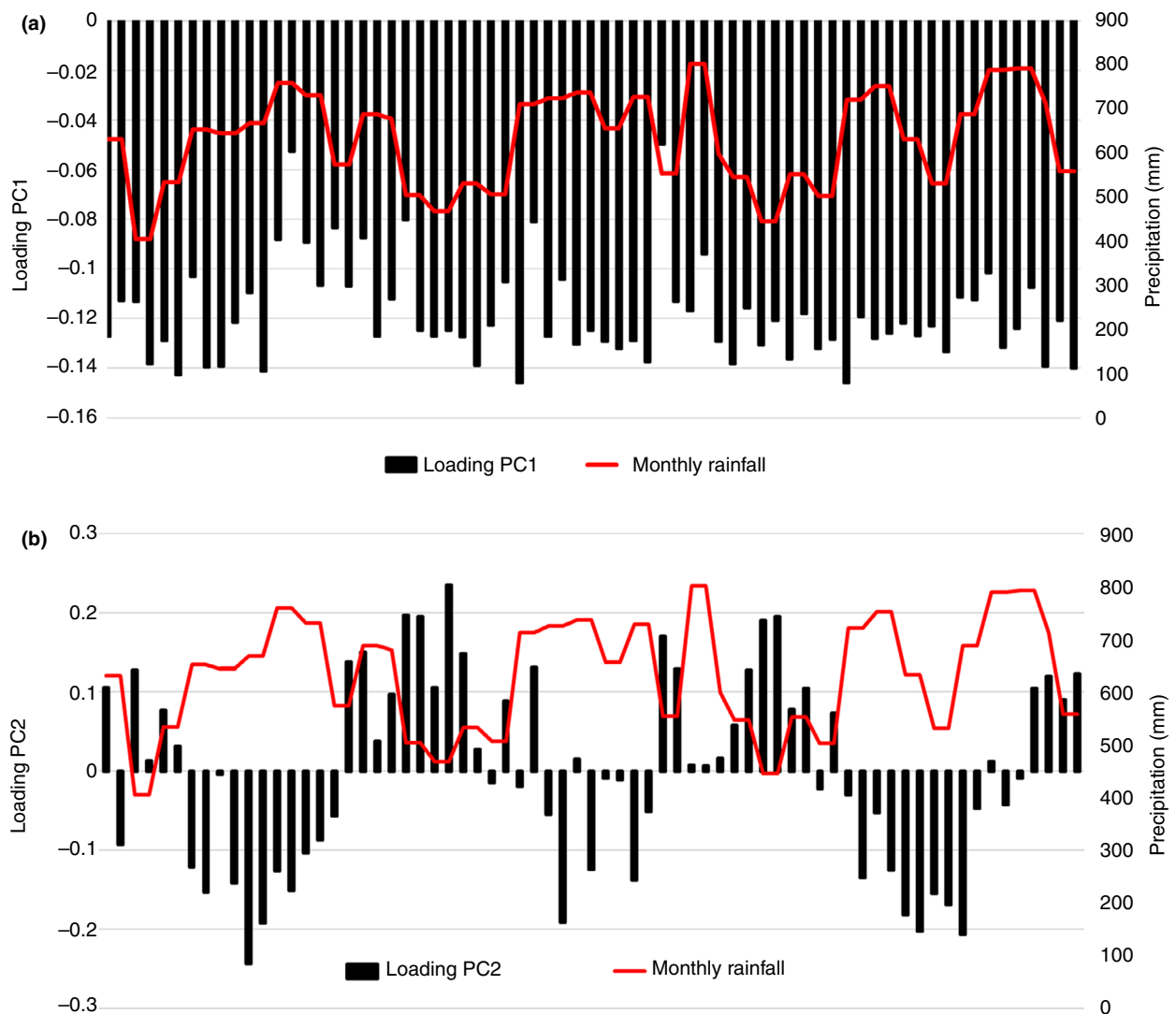
Regarding environmental similarity on species niches in the Colombian Pacific region, a slight degree of



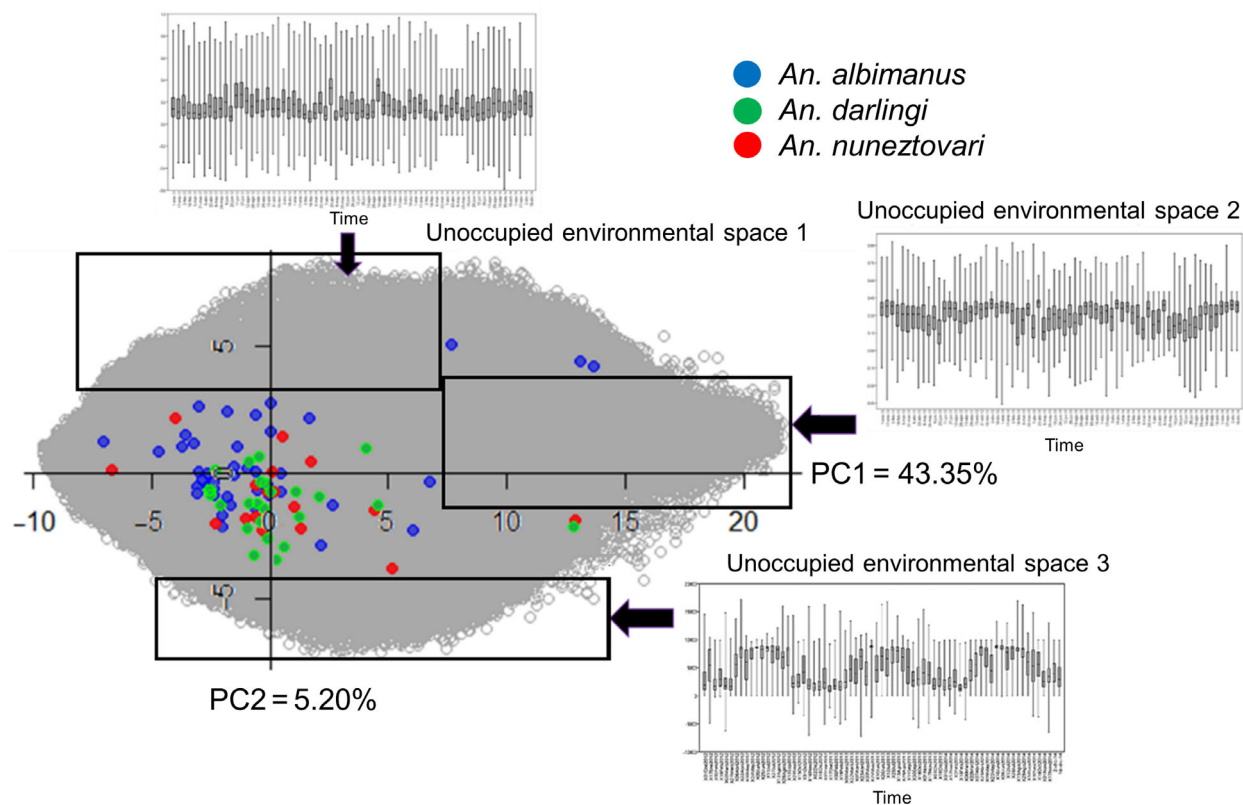
**Figure 2** Potential geographic distribution for (a) *Anopheles albimanus*, (b) *Anopheles darlingi* and (c) *Anopheles nuneztovari* in the Colombian Pacific region. Blue, green and red dots represent presence records used for calibration of the models for the three vectors. Suitable areas for the three vectors were 35.625%, 3.780% and 10.043%, respectively. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

environmental overlap was found for the three vectors. The Jaccard index indicated that the environmental overlap between *An. albimanus* vs. *An. nuneztovari* was of 0.341, *An. darlingi* vs. *An. nuneztovari* 0.227 and *An. darlingi* vs. *An. albimanus* 0.102 (Table S4). *Anopheles albimanus* had the highest niche amplitude compared to *An. darlingi* and *An. nuneztovari* (Figure 5). Background similarity tests revealed a high degree of similarity in geographic areas ( $p < 0.01$ ) between *An. darlingi* and *An. nuneztovari* ( $D = 0.516$ ) (Figure 6a),

whereas *An. albimanus* shared few geographic areas with *An. darlingi* ( $D = 0.208$ ) (Figure 6b) or *An. nuneztovari* ( $D = 0.204$ ) (Figure 6c). The distribution map of occupied areas showed that *An. albimanus* shared areas with *An. darlingi* and *An. nuneztovari*, corresponding to 0.676% and 1.489%, respectively; *An. darlingi* shared 2.553% of areas with *An. nuneztovari*, and the percentage of areas shared by the three vectors was 1.176% (Figure S1A–D). The distribution map for *An. albimanus* indicated that this was the vector with the greatest niche



**Figure 3** Loadings of the first two main components (PC1 and PC2) of the NDVI images in the Colombian Pacific region and their association with the average annual precipitation. (a) NDVI spatial variation. (b) NDVI temporal variation. The black bars indicate the contribution (positive or negative) of PC1 and PC2. The red lines represent the average monthly precipitation in the study area between January 2012 and December 2014 (data from <http://www.ideam.gov.co/solicitud-de-informacion>, June 2017). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Figure 4** Principal component analysis based on NDVI eigenvalues for the Colombian Pacific region. The cloud of grey circles represents NDVI eigenvalues for the region. Coloured dots are the NDVI eigenvalues corresponding to presence sites for the malaria vectors *An. albimanus*, *An. darlingi* and *An. nuneztovari*. The spaces enclosed in the boxes are available environments no occupied by the vectors, and the bar diagrams represent unoccupied environments. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

amplitude, with suitable areas in the Cauca river valley; during the visit for map validation, seven *An. albimanus* specimens were collected at La Paila locality in Zarzal municipality, while in Paso de la Bolsa locality, Jamundi municipality, none were detected (Figure S2).

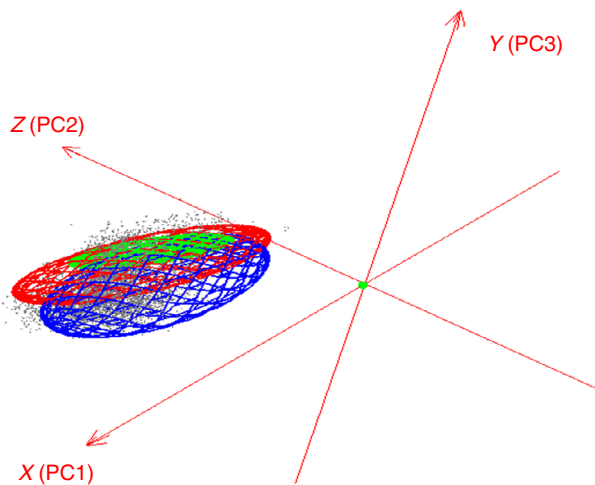
## Discussion

The use of the NDVI as remotely sensed environmental data, an indirect indicator of vegetation conditions, allowed characterising a portion of the existing fundamental niche [15] and potential distributions of the three Colombian main malaria vectors, *An. albimanus*, *An. darlingi* and *An. nuneztovari*, in the endemic Pacific region. NDVI proved to be a convenient tool for the identification of the suitable environments by these vectors; the models constructed detected differences in their distribution patterns in the region. Similarly, results of a previous study conducted in an important malaria

endemic region of north-western Colombia showed an association between vector occurrence and vegetation changes [14]. A few studies in South America that used climate data predicted environmental suitable areas for these vectors in the Pacific region [38,48,49]. However, the present work differs from the previous studies in producing geographic distribution maps based on remote sensing data that provide more detailed and accurate information than maps derived from climatic variables [50,51]. Also, as NDVI data estimate the photosynthetic capacity of vegetation, an indirect indicator of habitat conditions for mosquito development [30], these results could be used to prioritise areas with high malaria incidence in the region for control purposes.

*Anopheles albimanus* presented the widest distribution among the three vectors, with suitable areas in the Pacific coastlines and dry inter-Andean valleys of the Cauca and Patía rivers. It is known that *An. albimanus* is present on the Pacific shoreline [5,52], but prediction and later



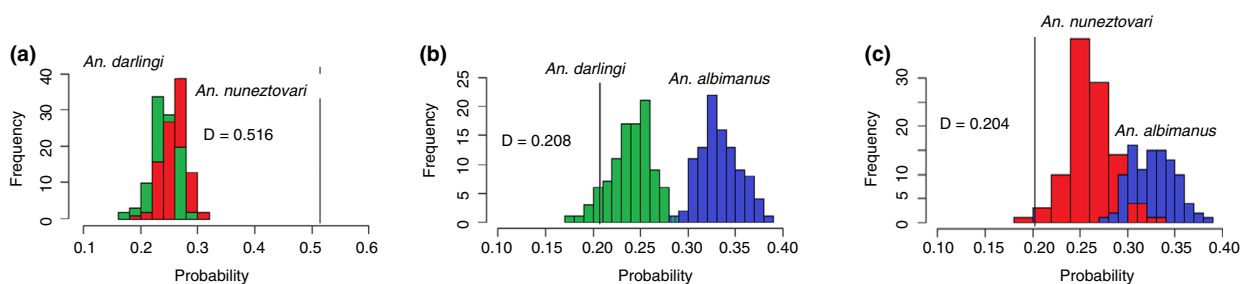


**Figure 5** Visualisation of the minimum volume ellipsoid for *An. albimanus*, *An. darlingi* and *An. nuneztovari* in the Colombian Pacific region. The cloud of grey points represents the environmental space of the first three main components (PC1, PC2 and PC3), and the ellipsoids represent the niche amplitude of *An. albimanus* (blue), *An. darlingi* (green) and *An. nuneztovari* (red). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

validation of the species in inter-Andean valleys suggest that this subregion have the ecologically appropriate conditions for its spreading. Furthermore, a previous report of *An. albimanus* at 995 m.a.s.l., in Villarica (Cauca Department), a municipality in proximity to the Cauca River [53] together with current model results, cautions on the possibility of *An. albimanus* occupying these territories and contributing to the resurgence of malaria in this subregion. The model for *An. darlingi* estimated suitable areas mainly along the Atrato and San Juan rivers (Chocó Department). An association of *An. darlingi* with riparian ecosystems in northwest Colombia was

previously shown [14]. This vector was found at agricultural and deforested areas by the Atrato river, in a north-western locality bordering the Pacific region [4]; also, a distribution model showed suitable areas for *An. darlingi* along the Cauca and Nechí rivers in north-western Colombia [14]. In the present work, environmentally suitable areas were predicted for *An. darlingi* in Cali city in west Colombia, where there are no reports of its presence. Therefore, these results should alert the authorities in charge of vector surveillance to the possibility of an accidental introduction. The model for *An. nuneztovari* showed suitable areas in the valleys of the Atrato and San Juan rivers (Chocó), and in Buenaventura and El Darién municipalities (Valle del Cauca). In relation to previous maps for *An. nuneztovari* [48,49], the current model predicted with more detail suitable areas in the Pacific region, for example in rural neighbourhoods of Buenaventura municipality. Five years ago, *An. nuneztovari* was collected in a rural locality of Buenaventura, where its larval habitats were fish farms and deforested flooded soils and it was found infected with *P. vivax* [4], which suggests a higher risk for malaria transmission in suitable areas for this vector.

During characterisation of vegetation photosynthetic activity, PC1 loading values were high and stable along the region. This may be related to the fact that the Colombian Pacific is second after the Amazon region in the number of plant biomass reserves [54]; there, natural and secondary forests predominate, mainly in the coasts and lowlands [55]. Furthermore, PC2 loading values provided relevant information about the temporal behaviour of vegetation in the study region, showing positive values in seasons of lower precipitation and negative values in higher precipitation. Possibly because leaf regeneration occurs and forest biomass augments with rainfall decrease and after humidity, light and solar radiation are more available [54].



**Figure 6** Background similarity diagrams of the geographic space for the three vectors in the Colombian Pacific region. (a) *An. darlingi* vs. *An. nuneztovari*. (b) *An. albimanus* vs. *An. darlingi*. (c) *An. albimanus* vs. *An. nuneztovari*. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

In the association between the time of collections and the images period, environments occupied by the vectors showed both, negative and low positive NDVI eigenvalues. Unoccupied environments had high positive and stable NDVI eigenvalues and represented primary forests, while other unoccupied regions presented NDVI eigenvalues with temporal variation and presumably correspond to altered forests [54]. These observations support the previous suggestion of NDVI data being an indirect indicator of the environmental conditions for mosquito development and the existence of basic requirements such as appropriate larval habitats [30]. Thus, the estimated low NDVI eigenvalues related to low canopy covers [54], may correspond to environments favourable for suitable larval habitats for the main vectors. Bare soils provide larval habitats for *An. albimanus*, such as water bodies near the coast and exposed to the sun [56]; habitats on the forest edges and riparian ecosystems are suitable for *An. darlingi* [14], and ponds and flooded soils used for livestock, agriculture and fish farming, for *An. nuneztovari* [57].

The background similarity test that measures geographic and environmental similitude showed a high co-occurrence for *An. darlingi* and *An. nuneztovari* in valleys of the San Juan and Atrato rivers. Co-occurrence of these two vectors has been previously reported in north-western localities [5], and shown in a potential distribution study for the Bajo Cauca region, also in NW Colombia, where these two vectors co-occur in some geographic areas [14]. In malaria endemic areas of NW Colombia, *An. darlingi* and *An. nuneztovari* have important roles in transmission [52]. A slight niche overlap was found for *An. albimanus* with *An. darlingi* and for *An. albimanus* with *An. nuneztovari*. The proportion of areas shared between *An. albimanus* and any of the other two vectors was very low, probably owed to the differences in vegetation. Low NDVI values for *An. albimanus* represent areas it occupies, with low vegetation cover and mangroves mainly on the coasts; the varied NDVI values for *An. darlingi* agree with the wooded and riverine environments with abundant vegetation in which it inhabits; whereas, the very low NDVI values for *An. nuneztovari* represent typical environments for the species such as flooded soils and areas highly altered by anthropic activities such as mining [3-5,57]. The results are also supported by findings in north-western Colombia, where *An. albimanus* occupied coastal environments in the Urabá region and *An. darlingi* riverine forests in the Bajo Cauca region [14]. Furthermore, the niche overlap test found low environmental similarity among *An. albimanus*, *An. darlingi* and *An. nuneztovari*. This result reflects the diverse vegetation cover types that these

vectors occupy. In a previous study in the Pacific region, the three vectors were collected in ecologically diverse localities; *An. darlingi* was detected at the forest borders in a northern Pacific locality, *An. nuneztovari* in flooded plains and deforested areas result of anthropic processes such as fish and farming in rural areas of a locality in central Pacific, and, *An. albimanus* in mangroves and wetland channels in south Pacific [4].

In general, the results demonstrated that NDVI, used as the environmental variable and an indirect indicator of vegetation conditions, allows characterising the existing fundamental niche and the potential distributions of the three main malaria vectors, *An. albimanus*, *An. darlingi* and *An. nuneztovari*, in the Colombian Pacific region. The NDVI data reflected the environmental heterogeneity that characterises the Pacific region. There were some limitations in our study such as not using NDVI data in a larger window or occurrence data from the following year to the NDVI data; however, these data were used given evidence in the literature indicating that in the region during this period, deforestation occurred at very low rates [31]. Finally, the information provided by the models is useful in the selection of priority areas for vector surveillance and the implementation of control interventions in this region to reduce malaria risk.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Maps of shared areas (percentage) for the three main vector species of the Colombian Pacific region. (A) *An. albimanus* and *An. darlingi* (0.676%). (B) *An. albimanus* and *An. nuneztovari* (1.489%). (C) *An. darlingi* and *An. nuneztovari* (2.553%). (D) The three vectors (1.176%).

**Figure S2.** Occupied and shared areas of the Colombian Pacific region by the three vectors as predicted by the models. (A) The Pacific region. Occupied areas represented by the colours blue (only *An. albimanus*), green (only *An. darlingi*) and red (only *An. nuneztovari*).

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Additional colours represent areas shared by two or three vector species. In grey, areas unoccupied by three vectors. (B) Location of sites sampled during the field trips for model validation.

**Table S1.** Statistics of model evaluation for *An. albimanus* in the Colombian Pacific region.

**Table S2.** Statistics of model evaluation for *An. darlingi* in the Colombian Pacific region.

**Table S3.** Statistics of model evaluation for *An. nuneztovari* in the endemic region of the Colombian Pacific.

**Table S4.** Niche overlap values for the three main malaria vectors of the Colombian Pacific region, based on the Jaccard similarity index.

**Corresponding Author** Margarita M. Correa, Grupo de Microbiología Molecular, Escuela de Microbiología, Universidad de Antioquia, Lab 5-430, Calle 70 No. 52-21, Medellín, Antioquia, Colombia. Tel.: +574 219 8489; Fax: +574 219 5481; E-mail: margarita.correa@udea.edu.co; margaritcorrea@gmail.com