A peer-reviewed version of this preprint was published in PeerJ on 16 August 2016.

View the peer-reviewed version (peerj.com/articles/2267), which is the preferred citable publication unless you specifically need to cite this preprint.

Murillo-Pacheco JI, Rös M, Escobar F, Castro-Lima F, Verdú JR, López-Iborra GM. (2016) Effect of wetland management: are lentic wetlands refuges of plant-species diversity in the Andean-Orinoco Piedmont of Colombia? PeerJ 4:e2267 https://doi.org/10.7717/peerj.2267
Effect of wetland management: Are lentic wetlands refuges of plant-species diversity in the Andean-Orinoco Piedmont of Colombia?

Johanna I. Murillo-Pacheco 1, 2, Matthias Rös 3, Federico Escobar Correspond., 4, Francisco Castro-Lima 5, José R Verdú 1, Germán M López-Iborra 6

1 I.U.I. CIBIO – Universidad de Alicante, Alicante, España
2 Facultad Ciencias Básicas e Ingeniería, Universidad de los Llanos, Grupo de investigación BIORINOQUIA, Villavicencio, Colombia
3 Instituto Politécnico Nacional, CONACYT Research Fellow, CIIDIR-Oaxaca, Oaxaca, Oaxaca, Mexico
4 Red de Ectología, Instituto de Ecología AC, Xalapa, Mexico
5 Independient researcher, Villavicencio, Meta, Colombia
6 Departamento de Ecología, Instituto de Investigación IMEM Ramón Margalef, Universidad de Alicante, Alicante, ALICANTE, Spain

Corresponding Author: Federico Escobar
Email address: federico.escobarf@gmail.com

Accelerated degradation of the wetlands and fragmentation of surrounding vegetation in the Andean-Orinoco Piedmont are the main threats to diversity and ecological integrity of these ecosystems; however, information on this topic is of limited availability. In this region, we evaluated the value of 37 lentic wetlands as reservoirs of woody and aquatic plants and, analyzed diversity and changes in species composition within and among groups defined according to management given by: 1) type (swamps, heronries, rice fields, semi-natural lakes, constructed lakes and fish farms) and, 2) origins (natural, mixed and artificial). A total of 506 plant species were recorded: 80% woody and 20% aquatic. Of these, 411 species (81%) were considered species typical of the area (Meta Piedmont distribution). Diversity patterns seem to be driven by high landscape heterogeneity and wetland management. The fish farms presented the highest diversity of woody plants, while swamps ranked highest for aquatic plant diversity. Regarding wetland origin, the artificial systems were the most diverse, but natural wetlands presented the highest diversity of typical species and can therefore be considered representative ecosystems at the regional scale. Our results suggest that lentic wetlands act as refuges for native vegetation of Meta Piedmont forest, hosting 55% of the woody of Piedmont species and 29% of the aquatic species of Orinoco basin. The wetlands showed a high species turnover and the results indicated that small wetlands (mean±SD: size = 11±18.7 ha), with a small area of surrounding forest (10±8.6 ha) supported high local and regional plant diversity. To ensure long-term conservation of lentic wetlands, it is necessary to develop management and conservation strategies that take both natural and created wetlands into
account.
Effect of wetland management: Are lentic wetlands refuges of plant-species diversity in the Andean-Orinoco Piedmont of Colombia?

Johanna Murillo-Pacheco¹,²*, Matthias Rös³*, Federico Escobar⁴*, Francisco Castro-Lima⁵, José R. Verdú¹, Germán M. López-Iborra⁶

¹ I.U.I. CIBIO – Universidad de Alicante, Campus San Vicente del Raspeig s/n, E-03690, Alicante, España.
² Grupo de investigación BIORINOQUIA, Facultad Ciencias Básicas e Ingeniería, Universidad de los Llanos, Campus Barcelona Km 12 vía Puerto López, Villavicencio, Colombia.
³ CONACYT Research Fellow, CIIDIR-Oaxaca, Instituto Politécnico Nacional, Mexico.
⁴ Instituto de Ecología A.C., A.P. 63 Xalapa, Veracruz, México.
⁵ Independent consultor. Carrera 51A No. 11-29 Villavicencio, Meta, Colombia.
⁶ Departamento de Ecología, Instituto de Investigación IMEM Ramón Margalef - Universidad de Alicante, Campus San Vicente del Raspeig, Alicante, España.

Corresponding author
*Federico Escobar
Instituto de Ecología A.C., A.P. 63 Xalapa, Veracruz, México.
federico.escobarf@gmail.com
ABSTRACT

Accelerated degradation of the wetlands and fragmentation of surrounding vegetation in the Andean-Orinoco Piedmont are the main threats to diversity and ecological integrity of these ecosystems; however, information on this topic is of limited availability. In this region, we evaluated the value of 37 lentic wetlands as reservoirs of woody and aquatic plants and, analyzed diversity and changes in species composition within and among groups defined according to management given by: 1) type (swamps, heronries, rice fields, semi-natural lakes, constructed lakes and fish farms) and, 2) origins (natural, mixed and artificial). A total of 506 plant species were recorded: 80% woody and 20% aquatic. Of these, 411 species (81%) were considered species typical of the area (Meta Piedmont distribution). Diversity patterns seem to be driven by high landscape heterogeneity and wetland management. The fish farms presented the highest diversity of woody plants, while swamps ranked highest for aquatic plant diversity. Regarding wetland origin, the artificial systems were the most diverse, but natural wetlands presented the highest diversity of typical species and can therefore be considered representative ecosystems at the regional scale. Our results suggest that lentic wetlands act as refuges for native vegetation of Meta Piedmont forest, hosting 55% of the woody of Piedmont species and 29% of the aquatic species of Orinoco basin. The wetlands showed a high species turnover and the results indicated that small wetlands (mean±SD: size = 11±18.7 ha), with a small area of surrounding forest (10±8.6 ha) supported high local and regional plant diversity. To ensure long-term conservation of lentic wetlands, it is necessary to develop management and conservation strategies that take both natural and created wetlands into account.

INTRODUCTION

The vegetation associated with wetlands is one of the most distinctive characteristics of aquatic ecosystems (Burton, Tiner & Gene 2009; Mitsch & Gosselink 2015). Plants are an important component of the dynamic of the aquatic systems and are considered an efficient indicator of
ecological integrity (Cronk & Fennessy 2001; Clément & Proctor 2009). However, it is known that biodiversity in wetlands is related to land use in the surrounding landscape in which they are immersed, as well as the type and intensity of management practiced (Wang et al., 2008; Mitsch & Gosselink 2015). Wetlands are known as strategic ecosystems for biodiversity (MEA 2005; Zedler & Kercher 2005), and they contribute to the maintenance of ecological functions across natural and human-dominated landscapes (e.g., in rice fields Rolon et al., 2008; Rolon & Maltchik 2009). Nevertheless, the role of wetlands as biodiversity reservoirs remains relatively poorly understood in Neotropical regions, particularly in the wetlands of the Orinoco river basin region (e.g., Díaz & Rosales 2006; Fernández, Bedoya & Madriñán 2015).

The Andean Piedmont of the Colombian Orinoco river basin once formed a continuous corridor of vegetation between the Eastern cordillera of the Andes, and the savannah ecosystems of the Llanos Orientales (Bates 1948; Molano 1998). This was a typical rainforest with swamplands that formed and maintained multiple wetlands (Bates 1948) within the region known as “Villavicencio pleistocene refuge” (Hernández et al., 1992). This region harbors over 3000 plant species (Minorta-Cely & Rangel-Ch. 2014) and is therefore considered one of the most diverse areas in northern South America. The Andean-Orinoco Piedmont has been heavily fragmented (Etter, McAlpine & Possingham 2008), and significant portions of the remaining vegetation are concentrated around wetlands. In this region, the natural wetlands (i.e., swamps and diverse flooded lands) and their surrounding vegetation have been reduced as a result of the expansion of the agricultural frontier, the urbanization and changes of land cover (i.e., Romero-Ruiz et al., 2004; Romero-Ruiz et al., 2009). Currently, lentic wetlands are distributed as isolated patches within an urban and rural landscape matrix, forming islands of aquatic ecosystems surrounded by Meta Piedmont vegetation, partly connected by riparian and flooded forests.
Wetlands are a conservation priority at regional (Lasso et al., 2014), national (MMA 2002) and global level (MEA 2005; Mitsch, Bernal & Hernandez 2015), and diversity studies play a key role in order to take efficient actions for their conservation and management (Ramsar 2007; Mitsch & Gosselink 2015). Wetland management and the different human activities involved modify plant diversity and composition (McKinney & Lockwood 1999). One effect of the fragmentation and simplification of forests is the dilution and biotic homogenization of native plant species assemblages (e.g., Magee et al., 1999; Chen et al., 2010). On the other hand, biotic differentiation is also possible as a consequence of isolation of the vegetation remnants (Arroyo-Rodríguez et al., 2013), and management practices (i.e., creation of wetlands, living fences, gardens), bringing with it the introduction of native and foreign species (Gallardo et al., 2015) which may affect negatively the diversity of typical species and the functionality of wetlands (Hager 2004; Ervin et al., 2006; Lambdon, Lloret & Hulme 2008).

The importance of type and origin of wetlands as drivers of biotic homogenization and differentiation of plant diversity is poorly known. In highly modified landscapes as in Andean Piedmont, vegetation is reduced to small fragments, many of them associated with lentic wetlands. Several studies highlight the role that these remnants have for the maintenance of plant diversity regardless whether these are natural (Flinn, Lechowicz & Waterway 2008) or created wetlands (Chester & Robson 2013). They may be considered as a refuge to species, in such a way that their associated vegetation could be acting as small forest patches that contribute highly to the regional diversity (Arroyo-Rodríguez et al., 2009).

In this study we evaluate the role of natural and created lentic wetlands as a refuge of plant diversity of the Meta Piedmont biome, and the influence of the wetland management in the diversity of woody and aquatic plants, focusing on two questions: 1) Are lentic wetlands, despite
its size, refuges of plant diversity? And, 2) how do the diversity and composition of plants associated with lentic wetlands change according to their management given by type and origin? We expect that wetland type has a strong influence on local and regional plant diversity, that natural wetlands retain the greatest plant diversity of Andean Piedmont and that lentic wetlands are potential reservoirs of plant diversity. This study presents the first estimates of plant diversity in lentic wetlands in the region, and aims to be a scientific baseline for the sustainable management and conservation of these wetlands and their associated vegetation.

**METHODS**

**Study area**

Andean Piedmont is a subregion of the Colombian Orinoco river basin, located in the East Andes in a transitional confluence area between the Andean mountains, and the Amazon and Savannah ecosystems, located within the physiographic unit known as Piedmont (Molano 1998; Romero-Ruiz et al., 2004; Rosales, Suárez & Lasso 2010; Minorta-Cely & Rangel-Ch. 2014). Our study area is found within the biome known as Meta Piedmont tropical humid zonobiome (THZ) (Romero-Ruiz et al., 2004), this covers 0.3% (83.493 ha) of the natural ecosystems of the Orinoco river Basin and is considered one of the most diverse ecosystems per unit area in the region. It is characterized by an altitude range of between 200–1100 m a.s.l., tropical very humid warm climate, mean annual temperature of 25°C and mean annual rainfall ranging from 2700 to 4600 mm, with the highest precipitation between April and June with monthly means superior to 500 mm (Minorta & Rangel. 2014) (see climograph in Fig 1).

This study was performed in the municipalities of Villavicencio, Puerto López, Restrepo and Cumará, Department of Meta (4°3’14.7”N - 73°42˚56.8”W and 3°59’41.1”N - 73°5’12.2”W)
Sampling was carried out in 37 lentic wetlands. They were grouped according to the type and origin of the wetlands, following our own proposed classification based on MMA (2002), RAMSAR (2012) and Lasso et al., (2014).

Wetland management was studied in six types of wetlands: 1) swamps (SW) are natural forest wetlands with emergent woody vegetation, they are flooded lands without a defined open body of water, associated with sources of other wetlands like streams or rivers; 2) heronries (HC) are natural swamplands with flooded areas and are characterized by the congregation of mixed species of breeding aquatic birds, specially herons and egrets; 3) rice fields (RF) are farms of irrigated rice crops that are mixed with natural water sources, channels and sometimes small dams, also they have fencerows with vegetation; 4) semi-natural lakes (SNL) were created after some management on natural wetlands that retain features of them and have tourist and recreational purposes; 5) constructed lakes (CL) are artificial wetlands that were built in its entirety, and are used as recreational lakes and dams; 6) fish farms (FF) are generally rectangular shaped ponds, created for aquaculture of freshwater fish production (see Table 1, for characteristic of wetlands).

We classified wetland types into three categories according to their origins: 1) natural: those that retain their original natural characteristics and where human intervention does not affect its natural dynamics (SW and HC); 2) mixed: those that have a natural origin but were transformed through human actions with extensive modification, so despite they can retain their natural features, they depend heavily on the constructed sections and facilities that regulate their hydric cycle (SNL and RF), and 3) artificial: wetlands that are completely human-made in places where no previous lentic wetland existed (CL and FF).
Sampling

We studied plant formations of woody and aquatic species. The sampling was carried out through standardized methods in each wetland. Woody plants (i.e., trees and shrubs) were sampled in four linear 50 x 2 m transects (0.04 ha), located as close as possible to the wetland shore, within a 200 m buffer around, and with a minimum distance of 100 m between transects. All individuals with a diameter at breast height (DBH) \( \geq \) 2.5 cm were recorded. Aquatic plants were sampled using ten 1x1 m plots placed in the flooded area of the wetland shore, where emergent vegetation was present (total of 320 plots, because in five wetlands we did not find aquatic species) with a minimum distance of 5 m between plots. In each plot, the percent cover of every species was measured. Only flowering plants (Angiosperms) and vascular cryptogams (Pteridophytes) were considered in this study. Species categorized as ‘typical’ were those having a distribution in the Meta Piedmont biome, and we refer to introduced exotic (from foreign countries) and native exotic species (with distribution in others native Colombian ecosystems) as ‘introduced’ plants. All plants were identified in the field by a specialist. The taxonomic species list is based on Cronquis (1981) and for introduced species on Alvarado & Gutiérrez (1997) and Cárdenas, Castaño & Cárdenas (2010).

Data analysis

Inventory completeness

We used the sample coverage estimator proposed by Chao & Jost (2012) to estimate the accuracy of inventories in each wetland, and in each type and origin category of the wetlands, using the iNEXT package for R (Hsieh, Ma & Chao 2015):
where \( n \) is the total number of plants, \( f_1 \) and \( f_2 \) are the numbers of singletons and doubletons of the sample. \( \hat{C}_m \) has values from 0 (minimal completeness) to 100\% (maximum completeness), and indicates the proportion of the ecological community that is represented by the species recorded and is used as a measure of sampling completeness (Chao & Jost 2012; Chao et al., 2014).

**Species diversity**

Diversity patterns were evaluated using Hill numbers \( ^qD \) (details in Jost 2006; Chao et al., 2014) for each wetland, within wetland type and origin, and among them. Hill numbers were calculated for order \( q = 0 \), corresponding to species richness (\( ^0D \)) and which is not sensitive to abundances (Jost 2006), and diversity of order \( q = 2 \), which is the inverse Simpson concentration index (\( ^2D \)), and can be interpreted as the number of ‘dominant’ species (Jost 2010a).

For both orders (\( ^0D \) and \( ^2D \)), diversity (\( \alpha \)-diversity) was calculated in three ways: local alpha diversity in each wetland (\( \alpha_w \)), total alpha diversity corresponding to pooled diversity of each type and origin category (\( \alpha \)), and mean alpha diversity (\( \bar{\alpha} \)) as average for each category of wetland type and origin. Finally, we obtained the regional (\( \gamma \)-diversity) as the total diversity of all wetlands.

Mean alpha diversity (\( \bar{\alpha} \)) among categories of type and origin of wetlands was compared based on its confidence intervals in which the absence of overlap between CI 95\% indicated significant differences (Cumming, Fidler & Vaux 2007). In order to compare the communities,
we calculated the magnitude of the difference in diversity among communities, which is used to know how many times is one sample more diverse than another sample (Jost 2006). The values of diversity in the two orders ($q = 0$ and $2$) were compared directly and also using the percentage of species diversity difference magnitude (%MD) between types and origins of wetlands. %MD

$$\text{%MD} = \left(\frac{qD_{\text{sample} > S} - qD_{\text{sample} < S}}{qD_{\text{sample} < S}}\right)\times 100$$

where $qD_{\text{sample} > S}$ is the sample with more diversity and $qD_{\text{sample} < S}$ is the sample of less diversity (modified from Cultid-Medina & Escobar 2016).

To evaluate species inequality, we calculated the relative logarithmic inequality (RLI), which is the logarithmic transformation of the inequality factor $IF_{0,q}$ (Jost 2010b):

$$RLI_{0,q} = \frac{(\ln IF_{0,q})}{(\ln S)}$$

where $S$ is the total alpha diversity and $IF_{0,2}$ is the inequality factor ($IF_{0,2} = 0D^{2}/D$). When $RLI_{0,q}$ is 0, it has maximum equality, when it is 1, it indicates maximum inequality (see details in Jost 2010b).

**Compositional similarity**

We measured compositional similarity $qCS$ (Jost 2007) within and among categories of type and origin wetlands.

$$qCS = \frac{{}^{q}D_{a} / {}^{q}D_{y} - \frac{1}{n}}}{{(1 - \frac{1}{n})}}$$


where $qD_\alpha$ is alpha diversity, $qD_\gamma$ is gamma diversity (corresponding to total alpha of each category), and $N$ is the number of samples; $qCS = 0$ when all samples are completely distinct, and $qCS = 1$ when all are identical. When $q = 0$, and $N = 2$, it equals the Jaccard index, and for $q = 2$ the Morisita-Horn-Index (Jost 2007).

**RESULTS**

We recorded a total of 506 vascular plant species from 85 families and 324 genera in the 37 lentic wetlands. 407 species were woody plants and 99 aquatic species. There were 411 (81%) typical species of Meta Piedmont and of the remaining 95 introduced species (19%), 43 corresponded to introduced exotic species and 52 to native exotic ones. Additionally, some of the species are categorized as threatened in red lists: *Cedrela odorata* as endangered in Colombia and vulnerable (IUCN 2013), also the *Bactris gasipaes* and *Syagrus sancona* in the national category as Vulnerable (VU A2ac).

**Completeness and diversity patterns**

The sampling coverage in each wetland was higher than 74%. Taking into account the wetlands according to the type and origin, completeness was greater than 92% (Table S1). Given the high inventory reliability, diversity comparisons were performed using the observed values.

There was a great variation in local diversity between wetlands in richness ($D_0$) and dominant species ($D_2$) (Figures 2-3 and Tables S1-S2), being highest in the semi-natural lake SNL6 (Lake Bioparque Ocarros, 94 species) and lowest in the constructed lake CL6 (Lake La Tonga, 11 species, see Table S2). There were no statistical differences in the mean alpha diversity ($\bar{\alpha}$) of woody and aquatic plants for both wetland type and origin (Figures 2-3 and
Total alpha diversity (α) showed differences among wetland types for both woody and aquatics plants (Figures 2-3 and Table S2). Woody species richness (\(0^D\)) was highest in FF (212 ± 12) and SNL (201 ± 13), and it was lowest in HC (78 ± 9) and RF (68 ± 6), presenting large richness difference magnitude between FF and RF (212%) as well as between SNL and RF (196%) (Fig 2a). The pattern was similar regarding dominant species (\(2^D\)), especially in HC, which showed the highest inequality (RLI\(_{0,2}\) = 0.52) (Fig 2b and Table S1), being the most dominant species *Mabea trianae* and *Bactris corossilla* with 29% and 16% of all individuals.

In aquatic plants there were also marked differences in total alpha diversity in the two orders evaluated (\(0^D\) and \(2^D\)), especially between SW and HC with a difference magnitude of 167% for species richness and 177% in terms of dominant species (Fig 2c). In general, the inequality values were low. SNL was the wetland type with greater dominance (RLI\(_{0,2}\) = 0.25, Fig 2d and S1 Table), where the presence of *Ludwigia inclinata*, with 16% of their plant coverage, stands out.

With regard to wetland origin, woody plants in artificial wetlands had higher species richness (\(0^D\)), mixed wetlands were more diverse regarding dominant species (\(2^D\)), and natural wetlands were the least diverse (Fig 3a, b), but had more inequality (RLI\(_{0,2}\) = 0.3). Species richness difference magnitude was 31% between artificial and natural wetlands, and dominant species difference magnitude was 101% between mixed and natural wetlands. In aquatic plants, the differences in diversity were low between origins (Fig 3c, d), as well as the values of inequality (RLI\(_{0,2}\) < 0.24). However, natural wetlands had greater species richness (\(0^D\)) and 14 species were exclusive in these.

**Compositional similarity (\(q^CS\))**
Compositional similarity in the whole landscape (i.e., for the entire set of wetlands studied) was low, but it showed a high variability within wetland types (Table S4). For both plant formations there was a high internal variability in the groups analyzed and $q_{CS}$ was lower within groups than among groups (Fig 4a, b). Taking into account the diversity of woody plants, constructed lakes (CL) were the wetland type with less similarity for all species ($0_{CS} = 0.07$), and heronries (HC) for dominant species ($2_{CS} = 0.01$), while rice fields (RF) showed higher similarity, which increased as $q$ increased ($0_{CS} = 0.23$ to $2_{CS} = 0.38$, Fig 4a). The pattern was similar in aquatic plants, it showed low similarity values, especially in CL and with maximum values in RF ($0_{CS} = 0.08$ and 0.32, respectively). All other wetland types had values lower than 0.17. Regarding dominant species, SW showed the lowest and HC the highest values ($2_{CS} = 0.1$ and 0.26 respectively, Fig 4b). Comparing CS of wetland types in woody and aquatic plants, we found a higher similarity among categories than within them in the two orders of similarity ($0_{2CS}$) (Figure 4a, b and Table S4).

Compositional similarity regarding the origin of wetlands in woody plants was low within the categories (natural, mixed and artificial) and intermediate among them. Natural wetlands had the highest similarity, especially in dominant species ($0_{CS} = 0.16$ and $2_{CS} = 0.27$) (Fig 4c). In the same way, in aquatic plants the compositional similarity was low within each origin category ($0_{CS} < 0.16$) and intermediate among them ($0_{CS} = 0.5$) for both richness ($0_{CS}$) and dominant species ($2_{CS}$) (Fig 4d and see Table S4).

**DISCUSSION**

This is the first comparative study on the diversity of plants in freshwater inland wetlands under different regimes of management in the Neotropical region. Although the total area of 37
wetlands studied (424 ha) and their forest area (435 ha) associated represent less than 1% of wetland coverage in the Orinoco region and 1% of the Meta Piedmont tropical humid zonobiome (Romero-Ruiz et al., 2004), our results indicated that these wetlands make a considerable contribution to local and regional diversity of woody and aquatic plants. The diversity of plants found represents around 55% of the woody species of the Meta Piedmont forest (Carvajal et al., 2007), 12% of the flowering plants (Minorta-Cely & Rangel-Ch. 2014), and 29% of aquatic plants (Fernández, Bedoya & Madriñán 2015) of the Colombian Orinoco river basin region. Typical Piedmont species showed high representation (81%), but the portion of introduced plants was considerable (19%), and had already an impact on diversity patterns and probably on the function of wetlands (Hager 2004; Lambdon, Lloret & Hulme 2008). The high diversity of the woody plants is related to forest of Meta Piedmont, where species of the Amazon and the Andes region converge, in addition to species associated with the eastern savannas (Molano 1998; Fernández et al., 2010), while aquatic plant diversity is related to the high complexity and variety of aquatic ecosystems in the Orinoco region (Rial 2014; Fernández, Bedoya & Madriñán 2015). Therefore, removal of these remnants of the landscape could endanger the conservation of plants of a region characterized by its high biodiversity (Bates 1948; Hernández et al., 1992; Molano 1998; Fernández et al., 2010).

Contrary to our expectation, the origin of natural wetlands had low diversity both in richness and dominant species. Which is associated to the fact that the heronries (HC) presented the lowest diversity between wetland types. Probably due to the accumulation of guano caused by the congregation of birds, which may have led to a naturally caused impoverishment of diversity due to the high nitrogen content of excrements (Ayarzagüena, Pérez & Ramo 1981), and it has been shown that a high bird activity can reduce the plant density of heronries (Weseloh...
Additionally, they are strongly altered by livestock which modifies the structure of the surrounding vegetation, since the increase of cattle grazing can affect negatively the wetland diversity (Junk 1993). On the contrary, swamps (SW) did not have such a low diversity, but lower than expected, as they are the most representative natural wetlands in the region (Lasso et al., 2014). The diversity of these wetlands can be related to the persistent human intervention along the time. Despite some swamps are locally protected, most of them are public lands, where chronic extraction of timber and urbanization processes in surrounding areas have been common (Machado, Rial & Lasso 2011).

The finding that artificial wetlands have a greater diversity of woody plants can be explained by the fact that both fish farms (FF) and constructed lakes (CL) are created by private enterprises, where owners have particular interests. Most of these wetlands were built on relict forest. Meanwhile, mixed wetlands retain a high diversity of species typical of Piedmont because they were developed on natural wetlands for recreational (semi-natural lakes - SNL) and agricultural (rice fields - RF) purposes, and its management allows to keep a portion of the diversity of native plants. The use of agrochemicals is often associated with the decline of plant diversity (Rolon & Maltchik 2009); although RF belonged to the group with higher diversity, we cannot exclude the possibility that without agrochemicals diversity would still be higher.

Our results show that the diversity patterns of plant species in and around wetlands are the result of both the heterogeneity of these wetlands at the landscape scale and human activities related with their management. Although wetlands are isolated systems, their heterogeneity and diversity have been attributed largely to the interaction with adjacent terrestrial and other aquatic ecosystems such as flooded and riparian forests (Mitsch & Gosselink 2015; Pott & Vila da Silva 2015), elements that contribute to connect and maintain diversity in human-dominated
landscapes as the Meta Piedmont (Molano 1998; Rangel-Ch 1998; Minorta-Cely & Rangel-Ch. 2014).

The results of this study support the importance of small forest fragments to conservation in human-dominated landscapes (e.g., Flinn, Lechowicz & Waterway 2008; Arroyo-Rodríguez et al., 2009). Despite the small size of the fragments of vegetation (<11 ha on average), the diversity of plants found is astonishing. In highly modified landscapes, conservation and management of a large number of small fragments can increase the differentiation in composition and reduce the probabilities of extinction. Similar results were found by Arroyo-Rodríguez et al., (2009) in Los Tuxtlas (Mexico), where even fragments less than 5 hectares were of great value to the maintenance of regional diversity. Small patches can be used as stepping stones that increase the landscape’s connectivity and facilitate movements among patches, and they may have complementary or supplementary resources that may favor survival of many animal species in fragmented landscapes (e.g., Brotons, Mönkkönen & Martin 2003; Pasinelli et al., 2008). Other authors have already highlighted the importance of small wetlands to regional plant diversity (Richardson et al., 2015), not only of natural wetlands (Flinn, Lechowicz & Waterway 2008) but also of small created wetlands (Chester & Robson 2013). Therefore, maintaining a diverse set of created wetlands can mitigate the reduction of diversity associated to natural wetlands loss, serving as shelter for birds and other organisms (e.g., Canals et al., 2011; Hapner et al., 2011). Similarly, they can contribute to hydrological dynamics and serve as areas for future ecological restoration (Moreno-Mateos et al., 2015).

Species composition and future scenarios
In our study compositional similarity was low (<0.5) compared to other studies in small forest patches in human modified landscapes, where higher CS-values were related to homogenization, and lower values to differentiation processes (See details in Arroyo-Rodríguez et al., 2013). The low compositional similarity values found can be explained by differences in type and origin of wetlands, being interesting that compositional similarity increased in most cases by comparing the dominant species (i.e., of the most abundant species), which makes clear the role of management of wetlands as a factor that determines taxonomic differentiation. We found higher differences in species composition within the wetland categories than among them, for both, origin and management. This pattern can be attributed to the high heterogeneity of wetland conditions, maybe due to external ecological factors and different disturbance levels (Clément & Proctor 2009). Other wetland diversity studies also reported high beta diversity related to spatial heterogeneity (Flinn, Lechowicz & Waterway 2008; Neiff et al., 2011). This could be attributed to the fact that in wetland remnants the habitat heterogeneity is the main driver for species richness, besides other attributes as its size (Shi et al., 2010). The naturally patchy distribution of wetlands also could contribute to a lower compositional similarity in these ecosystems (Dornelas, Soykan & Ugland 2011),

An important component in the composition of species in these lentic wetlands was that 19% corresponded to introduced plant species, half of them are exotic species from outside of Colombia, and 13 have invasive potential (Cárdenas, Castaño & Cárdenas 2010). Species introduction in this region is the result of: 1) planting of ornamental species as shade trees, flower beds and fruit trees for the embellishment predominantly of artificial and mixed wetlands (SNL, CL and FF); 2) sowing of forage species for livestock and, 3) the introduction of aquatic plants to decorate the lakes (CL) and for aquiculture uses (FF). Therefore, management of
wetlands determines the change of diversity with the introduction of exotic and native species. As it is known, the introduction of alien species is considered a threat to biodiversity (Alvarado & Gutiérrez 1997; Cárdenas, Castaño & Cárdenas 2010), and the ecological integrity of wetlands (MMA 2002; Gallardo et al., 2015) is one of the major drivers of biotic homogenization (Chen et al. 2010). That is why it requires the implementation of protocols for invasive species management in the creation and maintenance of wetlands (e.g., gardens, landscaping, fences living and restoration).

We suggest two opposed scenarios that may explain current plant diversity patterns in these lentic wetlands and may potentially contribute to understanding future conservation scenarios: 1) diversity is high because of the landscape heterogeneity, similar to the natural diversity pattern before fragmentation, and patches are sufficiently connected in order to maintain diversity in the long term and, 2) the low compositional similarity is a sign of independent dynamics of the wetland communities, hence plant populations are not sufficiently connected, increasing the probability that rare species may disappear from most wetlands (Gutzwiller & Flather 2011). This could decrease both local and regional diversity. Homogenization processes may cause local extinction of some species and lead to the dominance of few others (McKinney & Lockwood 1999; Arroyo-Rodriguez et al., 2013).

Management and conservation

Our results suggest that created lentic wetlands (i.e., artificial and mixed) can have a key role in plant diversity conservation by increasing the available habitat in the region for a variety of typical species. Nevertheless, the plant diversity in natural wetlands may not be replaced or equaled by artificial wetlands, yet the human-made wetlands are a way of safeguarding
biodiversity and partially compensate against rapid loss and transformation of natural wetlands (Yoon 2009; Ghermandi et al., 2010). Created wetlands have the capacity to sustain biodiversity or mitigate negative effects of wetland degradation (Galatowitsch & van der Valk 1996; Chester & Robson 2013), but in some cases their high diversity is the product of more early-successional stage species (Heaven, Gross & Gannon 2003).

Currently the Piedmont is a highly fragmented landscape (Romero-Ruiz et al., 2004; Etter, McAlpine & Possingham 2008; Romero-Ruiz et al., 2009) and conservation strategies for wetlands and forests have been reduced and inefficient. A new conservation model could be the promotion of ‘archipelago reserves’ (Halffter 2007). This approach is particularly useful in highly modified landscapes with high beta diversity, which could integrate the variability of the landscape and allow the conservation of high heterogeneity and plant diversity found in the region (Halffter 2005; 2007). Therefore, we strongly recommend including all wetland types into conservation and management programs, considering how each of them is already contributing to landscape diversity, and how some of them could be improved under appropriate management goals. Also, we suggest the implementation of conservation and restoration strategies according to the wetland type as well as the promotion of local policy for their regulation and management, integrating wetland ecology (Mitsch & Gosselink 2015) and sustainable utilization, particularly through promoting reconciliation between human land use and biodiversity from integration of the different social actors (i.e., citizens, stakeholders, policy makers and scientists). All these proposals are a way of safeguarding plant diversity of the Meta Piedmont forest species and the lentic wetlands.

ACKNOWLEDGEMENTS
We are grateful to Angelica Toro, Alvaro Velasquez, and Santiago Perez for the field assistance and help with the data storage. We would like to thank Liliana Ibañez and Maria del Sagrario Velasco Garcia for the English revision.

REFERENCES

- Alvarado F, Gutiérrez FDP. 1997. Especies hidrobiológicas continentales introducidas trasplantadas y su distribución en Colombia. Bogotá D. C.: Ministerio del Medio Ambiente.
- Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J. 2009. Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conservation Biology 23:729-739. DOI 10.1111/j.1523-1739.2008.01120.x
- Arroyo-Rodríguez V, Rós M, Escobar F, Melo FPL, Santos BA, Tabarelli M, Chazdon R. 2013. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology 101:1449-1458. DOI 10.1111/1365-2745.12153
- Ayarzagüena J, Pérez J, Ramo C. 1981. Los garceros de El Llano. Caracas, Venezuela: Cuadernos Lagoven.
- Bates M. 1948. Climate and Vegetation in the Villavicencio Region of Eastern Colombia. Geographical Review 38:555-574. DOI 10.2307/211443
- Brotons L, Mönkkönen M, Martin JL. 2003. Are fragments islands? landscape context and density-area relationships in Boreal forest birds. The American Naturalist 162:343-357. DOI 10.1086/376887
- Burton TM, Tiner RW, Gene EL. 2009. Ecology of wetlands. Encyclopedia of Inland Waters. Oxford: Academic Press, 507-515.
- Canals RM, Ferrer V, Iriarte A, Cárcamo S, Emeterio LS, Villanueva E. 2011. Emerging conflicts for the environmental use of water in high-valuable rangelands. Can livestock water ponds be managed as artificial wetlands for amphibians? Ecological Engineering 37:1443-1452. DOI 10.1016/j.ecoleng.2011.01.017
- Cárdenas D, Castaño N, Cárdenas J. 2010. Análisis de riesgo de especies de plantas introducidas para Colombia. In: Baptiste MP, Castaño N, Cárdenas D, Gutiérrez FP, Gil DL, Lasso CA, eds. Análisis de riesgo y propuesta de categorización de especies introducidas para Colombia. Bogotá D. C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 51-74.
- Carvajal L, Patarroyo J, Puentes D, Valero J. 2007. Caracterización florística y estructural del piedemonte llanero en el departamento del Meta: Corporación para el Desarrollo Sostenible del Área de Manejo Especial La Macarena-CORMACARENA. Universidad Distrital Francisco José de Caldas.
- Clément B, Proctor MCF. 2009. Ecological Dynamics I: Vegetation as Bioindicator and Dynamic Community. In: Maltby E, Barker T, eds. The Wetlands Handbook: Wiley-Blackwell, 282-303.
- Cronk JK, Fennessy MS. 2001. Wetland Plants: Biology and Ecology. Boca Raton: CRC Press
- Cronquist A. 1981. An Integrated System of Classification of Flowering Plants. New York: Columbia University Press.
- Cultid-Medina CA, Escobar F. 2016. Assessing the ecological response of Dung beetles in an agricultural landscape using number of individuals and biomass in diversity measures. Environmental Entomology 1-10. DOI 10.1093/ee/nvu219
- Cumming G, Fidler F, Vaux DL. 2007. Error bars in experimental biology. The Journal of Cell Biology 177:7-11. DOI 10.1083/jcb.200611141
Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* 84:45–67. DOI 10.1890/13-0133.1

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93:2533-2547. DOI 10.1890/11-1952.1

Chen H, Qian H, Spyreas G, Crossland M. 2010. Native-exotic species richness relationships across spatial scales and biotic homogenization in wetland plant communities of Illinois, USA. *Diversity and Distributions* 16:737-743. DOI 10.1111/j.1472-4642.2010.00679.x

Chester ET, Robson BJ. 2013. Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological Conservation* 166:64-75. DOI 10.1016/j.biocon.2013.06.016

Díaz W, Rosales J. 2006. Análisis florístico y descripción de la vegetación inundable de várzeas Orinoquenses en el bajo río Orinoco, Venezuela. *Acta Botánica Venezuélica* 29:39-68. DOI 10.2307/41740802

Dornelas M, Soykan CU, Ugland KI. 2011. Biodiversity and disturbance. In: Magurran AE, McGill B, eds. *Biological diversity Frontier in measurement and assessment*. New York: Oxford University press: Oxford.

Ervin G, Herman B, Bried J, Holly DC. 2006. Evaluating non-native species and wetland indicator status as components of wetlands floristic assessment. *Wetlands* 26:1114-1129. DOI 10.1672/0277-5212(2006)26[1114:ensawi]2.0.co;2

Etter A, Mc Alpine C, Possingham H. 2008. Historical patterns and drivers of landscape change in Colombia since 1500: a regionalized spatial approach. *Annals of the Association of American Geographers* 98:2-23. DOI 10.2307/25515096

Fernández Á, Gonto R, Rial A, Rosales J, Salamanca B, Córdoba M, Castro F, Alcázar C, García H, Ariza A. 2010. Flora y vegetación de la Cuenca del Orinoco. In: Lasso CA, Usma JS, Trujillo F, Rial A, eds. *2010 Biodiversidad de la cuenca del Orinoco: bases científicas para la identificación de áreas prioritarias para la conservación y uso sostenible de la biodiversidad*. Bogotá D. C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, WWF Colombia, Fundación Omacha, Fundación La Salle e Instituto de Estudios de la Orinoquia (Universidad Nacional de Colombia), 125-196

Fernández M, Bedoya AM, Madriñán S. 2015. Plantas acuáticas de las planicies inundables de la Orinoquia Colombiana. *Biota Colombiana* 16:96-105. http://www.redalyc.org/articulo.oa?id=49142418010

Flinn KM, Lechowicz MJ, Waterway MJ. 2008. Plant species diversity and composition of wetlands within an upland forest. *American Journal of Botany* 95:1216-1224. DOI 10.2307/41922368

Galatowitsch SM, van der Valk AG. 1996. The Vegetation of Restored and Natural Prairie Wetlands. *Ecological Applications* 6:102-112. DOI 10.2307/2269557

Gallardo B, Clavero M, Sánchez MI, Vilà M. 2015. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22:151–163. DOI 10.1111/gcb.13004

Gentry AH. 1982. Patterns of Neotropical Plant Species Diversity. In: Hecht MK, Wallace B, Prance GT, eds. *Evolutionary Biology*. New York: Springer US, 1-84.

Ghermandi A, van den Bergh JCJM, Brander LM, de Groot HLF, Nunes PALD. 2010. Values of natural and human-made wetlands: A meta-analysis. *Water Resources Research* 46:1-12. DOI 10.1029/2010wr009071

Gutzwiller KJ, Flather CH. 2011. Wetland features and landscape context predict the risk of wetland habitat loss. *Ecological Applications* 21:968-982. 10.2307/23021641

Hager H. 2004. Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia* 139:140-149. DOI 10.1007/s00442-004-1494-6
503 Halffter G. 2005. Towards a culture of biodiversity conservation. *Acta Zoológica Mexicana* 21:133-153.
504 Halffter G. 2007. Reservas archipiélago: Un nuevo tipo de área protegida. In: Halffter G, Guevara S, Melic A, eds. *Hacia una cultura de conservación biológica* Monografías del Tercer Milenio, 6, SEA Zaragoza, España: SEA, CONABIO, CONANP, CONACYT, INECOL, UNESCO-Mab, Ministerio de Medio Ambiente-Gobierno de España, 281-286.
505 Hapner JA, Reinartz JA, Fredlund GG, Leithoff KG, Cutright NL, Mueller WP. 2011. Avian succession in small created and restored wetlands. *Wetlands* 31:1089-1102. DOI 10.1007/s13157-011-0220-5
506 Heaven JB, Gross FE, Gannon AT. 2003. Vegetation comparison of a natural and a created emergent marsh wetland. *Southeastern Naturalist* 2:195-206. DOI 10.2307/3878138
507 Hernández J, Ortiz R, Walschburger T, Hurtado A. 1992. Estado de la biodiversidad en Colombia. In: Halffter G, ed. *La diversidad biológica de Iberoamérica: Acta zoológica Mexicana, Volumen Especial I*, 41-44.
508 Hsieh TC, Ma KH, Chao A. 2015. Package "iNEXT". Interpolation and extrapolation for species diversity. . 2.0.5 ed: Package for R.
509 IUCN. 2013. IUCN Red List of Threatened Species. Version 2013.2. International Union for Conservation of Nature.
510 Jost L. 2006. Entropy and diversity. *Oikos* 113:363-375. DOI 10.1111/j.2006.0030-1299.14714.x
511 Jost L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427-2439. DOI 10.1890/06-1736.1
512 Jost L. 2010a. Independence of alpha and beta diversities. *Ecology* 91:1969-1974. DOI 10.1890/09-0368.1
513 Jost L. 2010b. The Relation between evenness and diversity. *Diversity* 2:207-232. DOI 10.3390/d2020207
514 Junk WJ. 1993. Wetlands of Tropical South America In: Whigham DF, Dykyjová D, Hejný S, eds. *Wetlands of the world: Inventory, ecology and management* Handbook of vegetation science. Dordrecht: Springer Science+Business Media, B.V., 679-740.
515 Lambdon PW, Lloret F, Hulme PE. 2008. Do non-native species invasions lead to biotic homogenization at small scales? The similarity and functional diversity of habitats compared for alien and native components of Mediterranean floras. *Diversity and Distributions* 14:774-785. DOI 10.1111/j.1472-4642.2008.00490.x
516 Lasso CA, Rial A, Colonello G, Machado-Allison A, Trujillo F. 2014. XI. *Humedales de la Orinoquia (Colombia-Venezuela).* Serie editorial recursos hidrobiológicos y pesqueros continentales de Colombia. Bogotá D. C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.
517 Machado A, Rial A, Lasso CA. 2011. Amenazas e impactos sobre la biodiversidad y los ecosistemas acuáticos de la Orinoquia Venezolana. Estudio de caso. In: Lasso CA, Rial A, Matallana C, Ramirez W, Señaris J, Díaz-Pulido A, Corzo G, Machado-Allison A, eds. *Biodiversidad de la cuenca del Orinoco II Áreas prioritarias para la conservación y uso sostenible*. Bogotá D. C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Ministerio del Ambiente, Vivienda y Desarrollo Territorial, WWF Colombia, Fundación Omacha, Fundación La Salle de Ciencias Naturales e Instituto de Estudios de la Orinoquia, 42-61.
518 Magee T, Ernst T, Kentula M, Dwire K. 1999. Floristic comparison of freshwater wetlands in an urbanizing environment. *Wetlands* 19:517-534. DOI 10.1007/bf03161690
519 McKinney ML, Lockwood JL. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450-453. DOI 10.1016/S0169-5347(99)01679-1
520 MEA. 2005. *Ecosystems and human well-being: wetlands and water-synthesis*. Washington: Millenium Ecosystem Assessment. World Resource Institute.
Minorta-Cely V, Rangel-Ch. JO. 2014. La riqueza y la diversidad de las plantas con flores de la Orinoquía Colombiana. In: Rangel-Ch. JO, ed. Colombia Diversidad Biótica XIV La región de la Orinoquia de Colombia. Bogotá D. C.: Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, 237-418.

Minorta V, Rangel. JO. 2014. El clima de la Orinoquía Colombiana. In: Rangel JO, ed. Colombia Diversidad Biótica XIV La región de la Orinoquia de Colombia. Bogotá D. C.: Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales, 153-206.

Mitsch WJ, Bernal B, Hernandez ME. 2015. Ecosystem services of wetlands. International Journal of Biodiversity Science, Ecosystem Services & Management 11:1-4. DOI 10.1080/21513732.2015.1006250

Mitsch WJ, Gosselink JG. 2015. Wetlands. Hoboken: NJ: John Wiley & Sons, Inc.

MMA. 2002. Política nacional para humedales interiores de Colombia estrategias para su conservación y uso racional. Ministerio del Medio Ambiente Consejo Nacional Ambiental. Bogotá D. C.

Molano J. 1998. Biogeografía de la Orinoquía Colombiana. In: Fajardo D, ed. Colombia Orinoco. Bogotá D. C.: Fondo FEN Colombia, 69-101.

Moreno-Mateos D, Meli P, Vara-Rodríguez MI, Aronson J. 2015. Ecosystem response to interventions: lessons from restored and created wetland ecosystems. Journal of Applied Ecology 52:1528-1537. DOI 10.1111/1365-2664.12518

Neiff JJ, Casco SL, Cózar A, Poi de Neiff ASG, Ubeda B. 2011. Vegetation diversity in a large Neotropical wetland during two different climatic scenarios. Biodiversity and Conservation 20:2007-2025. DOI 10.1007/s10531-011-0071-7

Pasinelli G, Mayer C, Gouskov A, Schiegk K. 2008. Small and large wetland fragments are equally suited breeding sites for a ground-nesting passerine. Oecologia 156:703-714. DOI 10.1007/s00442-008-1013-2

Pott A, Vila da Silva JS. 2015. Terrestrial and aquatic vegetation diversity of the Pantanal wetland. Springer Berlin Heidelberg, 1-21.

Ramsar. 2007. Inventario, evaluación y monitoreo: Marco integrado para el inventario, la evaluación y el monitoreo de humedales. Manuales Ramsar para el uso racional de los humedales 3 edn 11 vol. 3 ed. Gland, Suiza: Secretaría de la convención Ramsar

Ramsar. 2012. Definición de "humedales" y sistema de clasificación de tipos de humedales de la Convención de Ramsar. Gland, Suiza.: Secretaría de la convención Ramsar.

Rangel-Ch JO. 1998. Flora Orinoquense. In: Fajardo M, Dominguez C, Molano BJ, Rangel O, Defler T, Rodriguez JV, I. Cdf, Gomez AJ, Publio PH, Barona B, Mejia. M, Romero M, Diaz ME, Galeano O, L. P-B, eds. Colombia Orinoco. Bogotá: Fondo FEN Colombia, 103-133.

Rial A. 2014. 3. Plantas acuáticas: utilidad para la identificación y definición de límites en humedales de la Orinoquia. In: Lasso CA, Rial A, Colonnelly G, Machado-Allison A,Trujillo F, eds. XI Humedales de la Orinoquia (Colombia- Venezuela) Serie Editorial Recursos Hidrobiológicos y Pesqueros Continentales de Colombia. Bogotá D. C.: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Richardson SJ, Clayton R, Rance BD, Broadbent H, McGlone MS, Wilmhurst JM. 2015. Small wetlands are critical for safeguarding rare and threatened plant species. Applied Vegetation Science 18:230-241. DOI 10.1111/avsc.12144

Rolon AS, Lacerda T, Maltchik L, Guadagnin DL. 2008. Influence of area, habitat and water chemistry on richness and composition of macrophyte assemblages in southern Brazilian wetlands. Journal of Vegetation Science 19:221-228. DOI 10.3170/2008-8-18359

Rolon AS, Maltchik L. 2009. Does flooding of rice fields after cultivation contribute to wetland plant conservation in southern Brazil? Applied Vegetation Science 13:26-35. DOI 10.1111/j.1654-109X.2009.01046.x
Romero-Ruiz M, Galindo G, Otero J, Armenteras D. 2004. *Ecosistemas de la cuenca del Orinoco Colombiano*. Bogotá D. C.: Instituto de Investigaciones en Recursos Biológicos Alexander von Humboldt - IAvH e Instituto Geográfico Agustín Codazzi - IGAC.

Romero-Ruiz MH, Maldonado-Ocampo JA, Bogotá-Gregory JD, Usma JS, Umaña-Villaveces AM, Murillo-Pacheco JI, Payán E. 2009. *Informe sobre el estado de la biodiversidad en Colombia 2007-2008: piedemonte Orinoquense, sabanas y bosques asociados al norte del río Guaviare*. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Rosales J, Suárez CF, Lasso CA. 2010. *Descripción del medio natural de la cuenca del Orinoco*. In: Lasso CA, Usma JS, Trujillo F, Rial A, eds. *Biodiversidad de la cuenca del Orinoco: bases científicas para la identificación de áreas prioritarias para la conservación y uso sostenible de la biodiversidad*. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, WWF Colombia, Fundación Omacha, Fundacion La Salle e Instituto de Estudios de la Orinoquia, 51-73.

Shi J, Ma K, Wang J, Zhao J, He K. 2010. Vascular plant species richness on wetland remnants is determined by both area and habitat heterogeneity. *Biodiversity and Conservation* 19:1279-1295. DOI 10.1007/s10531-009-9757-5

Wang Y, Hong W, Wu C, He D, Lin S, Fan H. 2008. Application of landscape ecology to the research on wetlands. *Journal of Forestry Research* 19:164-170. 10.1007/s11676-008-0029-0

Weseloh DV, Brown RT. 1971. Plant Distribution within a Heron Rookery. *American Midland Naturalist* 86:57-64.

Yoon C. 2009. Wise use of paddy rice fields to partially compensate for the loss of natural wetlands. *Paddy and Water Environment* 7:357-366. DOI 10.1007/s10333-009-0178-6

Zedler JB, Kercher S. 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30:39-74. DOI 10.1146/annurev.energy.30.050504.144248
Table 1. Lentic wetlands studied. Size refers to total area of water surface (424 ha) and forest coverage (435 ha) in a 500m buffer calculated from centroid of each wetland. Mean ± SD shown in brackets.

| Wetland type            | Origin | No. of wetlands | Size (ha)         | Forest (ha)     |
|-------------------------|--------|-----------------|-------------------|-----------------|
| Swamps (SW)             | Natural| 6               | 76.7 (12.8±17.8)  | 68.7 (11.4±8.6) |
| Heronries (HC)          | Natural| 4               | 6.9 (1.7±1.2)     | 19.1 (4.8±6.8)  |
| Rice fields (RF)        | Mixed  | 3               | 188.3 (62.8±18.9) | 27.9 (9.3±15.6) |
| Semi-natural lakes (SNL)| Mixed  | 6               | 25.5 (4.2±2.6)    | 77.7 (12.9±7.2) |
| Constructed lakes (CL)  | Artificial| 9           | 20.5 (2.3±2.1)    | 95.4 (10.6±7.4) |
| Fish farms (FF)         | Artificial| 9           | 106.2 (11.8±15.9) | 146.4 (16.3±12.4)|
The climograph shows the mean temperature (line) and precipitation (bars) of Villavicencio municipality.

Fig 1. Localization of lentic wetlands at the Meta Piedmont in Colombian Andean-Orinoco region. Municipalities of Villavicencio, Restrepo, Cumaral and Puerto López with urban center.
Fig 2. Alpha diversity of woody and aquatic plants according to wetland types. Wetland types: swamps (SW); heronries (HR); rice fields (RF); semi-natural lakes (SNL); constructed lakes (CL); fish farms (FF). Diversity using Hill numbers: species richness ($\alpha$D) and dominant species ($\gamma$D). Mean alpha diversity are gray points and local alpha diversity black points. Note that despite similar mean alpha diversity, the contribution of each wetland type to total alpha diversity is different.
Fig 3. Alpha diversity of woody and aquatic plants within and among wetland origins.

Diversity using Hill numbers: species richness ($D$) and dominant species ($\gamma D$). Mean alpha diversity are gray points and local alpha diversity black points.
Fig 4. Compositional similarity ($q_{CS}$) of species richness ($0D$) and dominant species ($2D$) of woody and aquatic plants within and among wetland types (WT) and origins (WO).

Wetland types: Swamps (SW); heronries (HR); rice fields (RF); semi-natural lakes (SNL); constructed lakes (CL); fish farms (FF).