Effect of wetland management: Are lentic wetlands refuges of plant-species diversity in the Andean-Orinoco Piedmont of Colombia?

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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.

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2   **Andean-Orinoco Piedmont of Colombia?**

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25   **ABSTRACT**

26   Accelerated degradation of the wetlands and fragmentation of surrounding vegetation in the Andean-

27   Orinoco Piedmont are the main threats to diversity and ecological integrity of these ecosystems; however,

28   information on this topic is of limited availability. In this region, we evaluated the value of 37 lentic

29   wetlands as reservoirs of woody and aquatic plants and, analyzed diversity and changes in species

30   composition within and among groups defined according to management given by: 1) type (swamps,

31   heronries, rice fields, semi-natural lakes, constructed lakes and fish farms) and, 2) origins (natural, mixed

32   and artificial). A total of 506 plant species were recorded: 80% woody and 20% aquatic. Of these, 411

33   species (81%) were considered species typical of the area (Meta Piedmont distribution). Diversity patterns

34   seem to be driven by high landscape heterogeneity and wetland management. The fish farms presented

35   the highest diversity of woody plants, while swamps ranked highest for aquatic plant diversity. Regarding

36   wetland origin, the artificial systems were the most diverse, but natural wetlands presented the highest

37   diversity of typical species and can therefore be considered representative ecosystems at the regional

38   scale. Our results suggest that lentic wetlands act as refuges for native vegetation of Meta Piedmont

39   forest, hosting 55% of the woody of Piedmont species and 29% of the aquatic species of Orinoco basin.

40   The wetlands showed a high species turnover and the results indicated that small wetlands (mean±SD:

41   size = 11±18.7 ha), with a small area of surrounding forest (10±8.6 ha) supported high local and regional

42   plant diversity. To ensure long-term conservation of lentic wetlands, it is necessary to develop

43   management and conservation strategies that take both natural and created wetlands into account.

44

45   **INTRODUCTION**

46   The vegetation associated with wetlands is one of the most distinctive characteristics of aquatic

47   ecosystems (Burton, Tiner & Gene 2009; Mitsch & Gosselink 2015). Plants are an important

48   component of the dynamic of the aquatic systems and are considered an efficient indicator of

49 ecological integrity (Cronk & Fennessy 2001; Clément & Proctor 2009). However, it is known

50 that biodiversity in wetlands is related to land use in the surrounding landscape in which they are

51 immersed, as well as the type and intensity of management practiced (Wang et al., 2008; Mitsch

52 & Gosselink 2015). Wetlands are known as strategic ecosystems for biodiversity (MEA 2005;

53 Zedler & Kercher 2005), and they contribute to the maintenance of ecological functions across

54 natural and human-dominated landscapes (e.g., in rice fields Rolon et al., 2008; Rolon &

55 Maltchik 2009). Nevertheless, the role of wetlands as biodiversity reservoirs remains relatively

56 poorly understood in Neotropical regions, particularly in the wetlands of the Orinoco river basin

57 region (e.g., Díaz & Rosales 2006; Fernández, Bedoya & Madriñán 2015).

58   The Andean Piedmont of the Colombian Orinoco river basin once formed a continuous

59 corridor of vegetation between the Eastern cordillera of the Andes, and the savannah ecosystems

60 of the Llanos Orientales (Bates 1948; Molano 1998). This was a typical rainforest with

61 swamplands that formed and maintained multiple wetlands (Bates 1948) within the region

62 known as "Villavicencio pleistocene refuge" (Hernández et al., 1992). This region harbors over

63 3000 plant species (Minorta-Cely & Rangel-Ch. 2014) and is therefore considered one of the

64 most diverse areas in northern South America. The Andean-Orinoco Piedmont has been heavily

65 fragmented (Etter, McAlpine & Possingham 2008), and significant portions of the remaining

66 vegetation are concentrated around wetlands. In this region, the natural wetlands (i.e., swamps

67 and diverse flooded lands) and their surrounding vegetation have been reduced as a result of the

68 expansion of the agricultural frontier, the urbanization and changes of land cover (i.e., Romero-

69 Ruiz et al., 2004; Romero-Ruiz et al., 2009). Currently, lentic wetlands are distributed as isolated

70 patches within an urban and rural landscape matrix, forming islands of aquatic ecosystems

71 surrounded by Meta Piedmont vegetation, partly connected by riparian and flooded forests.

72   Wetlands are a conservation priority at regional (Lasso et al., 2014), national (MMA

73   2002) and global level (MEA 2005; Mitsch, Bernal & Hernandez 2015), and diversity studies

74   play a key role in order to take efficient actions for their conservation and management (Ramsar

75   2007; Mitsch & Gosselink 2015). Wetland management and the different human activities

76   involved modify plant diversity and composition (McKinney & Lockwood 1999). One effect of

77   the fragmentation and simplification of forests is the dilution and biotic homogenization of

78   native plant species assemblages (e.g., Magee et al., 1999; Chen et al., 2010). On the other hand,

79   biotic differentiation is also possible as a consequence of isolation of the vegetation remnants

80   (Arroyo-Rodríguez et al., 2013), and management practices (i.e., creation of wetlands, living

81   fences, gardens), bringing with it the introduction of native and foreign species (Gallardo et al.,

82   2015) which may affect negatively the diversity of typical species and the functionality of

83   wetlands (Hager 2004; Ervin et al., 2006; Lambdon, Lloret & Hulme 2008).

84   The importance of type and origin of wetlands as drivers of biotic homogenization and

85   differentiation of plant diversity is poorly known. In highly modified landscapes as in Andean

86   Piedmont, vegetation is reduced to small fragments, many of them associated with lentic

87   wetlands. Several studies highlight the role that these remnants have for the maintenance of plant

88   diversity regardless whether these are natural (Flinn, Lechowicz & Waterway 2008) or created

89   wetlands (Chester & Robson 2013). They may be considered as a refuge to species, in such a

90   way that their associated vegetation could be acting as small forest patches that contribute highly

91   to the regional diversity (Arroyo-Rodríguez et al., 2009).

92   In this study we evaluate the role of natural and created lentic wetlands as a refuge of

93   plant diversity of the Meta Piedmont biome, and the influence of the wetland management in the

94   diversity of woody and aquatic plants, focusing on two questions: 1) Are lentic wetlands, despite

95   its size, refuges of plant diversity? And, 2) how do the diversity and composition of plants

96   associated with lentic wetlands change according to their management given by type and origin?

97   We expect that wetland type has a strong influence on local and regional plant diversity, that

98   natural wetlands retain the greatest plant diversity of Andean Piedmont and that lentic wetlands

99   are potential reservoirs of plant diversity. This study presents the first estimates of plant diversity

100   in lentic wetlands in the region, and aims to be a scientific baseline for the sustainable

101   management and conservation of these wetlands and their associated vegetation.

102

103   **METHODS**

104   **Study area**

105   Andean Piedmont is a subregion of the Colombian Orinoco river basin, located in the

106   East Andes in a transitional confluence area between the Andean mountains, and the Amazon

107   and Savannah ecosystems, located within the physiographic unit known as Piedmont (Molano

108   1998; Romero-Ruiz et al., 2004; Rosales, Suárez & Lasso 2010; Minorta-Cely & Rangel-Ch.

109   2014). Our study area is found within the biome known as Meta Piedmont tropical humid

110   zonobiome (THZ) (Romero-Ruiz et al., 2004), this covers 0.3% (83.493 ha) of the natural

111   ecosystems of the Orinoco river Basin and is considered one of the most diverse ecosystems per

112   unit area in the region. It is characterized by an altitude range of between 200–1100 m a.s.l.,

113   tropical very humid warm climate, mean annual temperature of 25°C and mean annual rainfall

114   ranging from 2700 to 4600 mm, with the highest precipitation between April and June with

115   monthly means superior to 500 mm (Minorta & Rangel. 2014) (see climograph in Fig 1).

116   This study was performed in the municipalities of Villavicencio, Puerto López, Restrepo

117   and Cumaral, Department of Meta (4°3´14.7¨N - 73°42´56.8¨W and 3°59´41.1¨N - 73°5´12.2¨W)

118   (Fig 1). Sampling was carried out in 37 lentic wetlands. They were grouped according to the type

119   and origin of the wetlands, following our own proposed classification based on MMA (2002),

120   RAMSAR (2012) and Lasso et al., (2014).

121   Wetland management was studied in six types of wetlands: 1) swamps (SW) are natural

122   forest wetlands with emergent woody vegetation, they are flooded lands without a defined open

123   body of water, associated with sources of other wetlands like streams or rivers; 2) heronries (HC)

124   are natural swamplands with flooded areas and are characterized by the congregation of mixed

125   species of breeding aquatic birds, specially herons and egrets; 3) rice fields (RF) are farms of

126   irrigated rice crops that are mixed with natural water sources, channels and sometimes small

127   dams, also they have fencerows with vegetation; 4) semi-natural lakes (SNL) were created after

128   some management on natural wetlands that retain features of them and have tourist and

129   recreational purposes; 5) constructed lakes (CL) are artificial wetlands that were built in its

130   entirety, and are used as recreational lakes and dams; 6) fish farms (FF) are generally rectangular

131   shaped ponds, created for aquaculture of freshwater fish production (see Table 1, for

132   characteristic of wetlands).

133   We classified wetland types into three categories according to their origins: 1) natural:

134   those that retain their original natural characteristics and where human intervention does not

135   affect its natural dynamics (SW and HC); 2) mixed: those that have a natural origin but were

136   transformed through human actions with extensive modification, so despite they can retain their

137   natural features, they depend heavily on the constructed sections and facilities that regulate their

138   hydric cycle (SNL and RF), and 3) artificial: wetlands that are completely human-made in places

139   where no previous lentic wetland existed (CL and FF).

140

Sampling

141   **Sampling**

142   We studied plant formations of woody and aquatic species. The sampling was carried out

143   through standardized methods in each wetland. Woody plants (i.e., trees and shrubs) were

144   sampled in four linear 50 x 2 m transects (0.04 ha), located as close as possible to the wetland

145   shore, within a 200 m buffer around, and with a minimum distance of 100 m between transects.

146   All individuals with a diameter at breast height (DBH) $\geq$ 2.5 cm were recorded. Aquatic plants

147   were sampled using ten 1x1 m plots placed in the flooded area of the wetland shore, where

148   emergent vegetation was present (total of 320 plots, because in five wetlands we did not found

149   aquatic species) with a minimum distance of 5 m between plots. In each plot, the percent cover

150   of every species was measured. Only flowering plants (Angiosperms) and vascular cryptogams

151   (Pteridophytes) were considered in this study. Species categorized as 'typical' were those having

152   a distribution in the Meta Piedmont biome, and we refer to introduced exotic (from foreign

153   countries) and native exotic species (with distribution in others native Colombian ecosystems) as

154   'introduced' plants. All plants were identified in the field by a specialist. The taxonomic species

155   list is based on Cronquis (1981) and for introduced species on Alvarado & Gutiérrez (1997) and

156   Cárdenas, Castaño & Cárdenas (2010).

157

158   **Data analysis**

159   ***Inventory completeness***

160   We used the sample coverage estimator proposed by Chao & Jost (2012) to estimate the

161   accuracy of inventories in each wetland, and in each type and origin category of the wetlands,

162   using the iNEXT package for R (Hsieh, Ma & Chao 2015):

163

$$\hat{C}m = \left(1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]\right) * 100 \quad (1),$$

164

165

166   where n is the total number of plants, f_1 and f_2 are the numbers of singletons and doubletons of

167   the sample. $\hat{C}m$ has values from 0 (minimal completeness) to 100% (maximum completeness),

168   and indicates the proportion of the ecological community that is represented by the species

169   recorded and is used as a measure of sampling completeness (Chao & Jost 2012; Chao et al.,

170   2014).

171

172   ***Species diversity***

173   Diversity patterns were evaluated using Hill numbers ^qD (details in Jost 2006; Chao et al., 2014)

174   for each wetland, within wetland type and origin, and among them. Hill numbers were calculated

175   for order $q = 0$, corresponding to species richness (^0D) and which is not sensitive to abundances

176   (Jost 2006), and diversity of order $q = 2$, which is the inverse Simpson concentration index (^2D),

177   and can be interpreted as the number of 'dominant' species (Jost 2010a).

178   For both orders (^0D and ^2D), diversity (α-diversity) was calculated in three ways: local

179   alpha diversity in each wetland (α_w), total alpha diversity corresponding to pooled diversity of

180   each type and origin category (α), and mean alpha diversity ($\bar{\alpha}$) as average for each category of

181   wetland type and origin. Finally, we obtained the regional (γ-diversity) as the total diversity of

182   all wetlands.

183   Mean alpha diversity ($\bar{\alpha}$) among categories of type and origin of wetlands was compared

184   based on its confidence intervals in which the absence of overlap between CI 95% indicated

185   significant differences (Cumming, Fidler & Vaux 2007). In order to compare the communities,

186   we calculated the magnitude of the difference in diversity among communities, which is used to

187   know how many times is one sample more diverse than another sample (Jost 2006). The values

188   of diversity in the two orders ($q = 0$ and 2) were compared directly and also using the percentage

189   of species diversity difference magnitude (%MD) between types and origins of wetlands. %MD

190    $= [(^{q}D_{sample} > S - ^{q}D_{sample} < S)*100 / \, ^{q}D_{sample} < S]$, where $^{q}D_{sample} > S$ is the sample with more

191   diversity and $^{q}D_{sample} < S$ is the sample of less diversity (modified from Cultid-Medina &

192   Escobar 2016).

193   To evaluate species inequality, we calculated the relative logarithmic inequality (RLI),

194   which is the logarithmic transformation of the inequality factor $IF_{0,q}$ (Jost 2010b):

195

196    $$RLI_{0,q} = \frac{(In \, IF_{0,q})}{(In \, S)} \quad (3),$$

197

198   where S is the total alpha diversity and $IF_{0,2}$ is the inequality factor ($IF_{0,2} = {^{0}D}/{^{2}D}$). When $RLI_{0,q}$ is

199   0, it has maximum equality, when it is 1, it indicates maximum inequality (see details in Jost

200   2010b).

201

202   ***Compositional similarity***

203   We measured compositional similarity ^{q}CS (Jost 2007) within and among categories of type and

204   origin wetlands.

205

206    $$^{q}CS = \frac{(^{q}D_{a}/^{q}D_{\gamma} - \frac{1}{N})}{\left(1 - \frac{1}{N}\right)} \quad (4)$$

207

208   where $^qD\alpha$ is alpha diversity, $^qD\gamma$ is gamma diversity (corresponding to total alpha of each

209   category), and N is the number of samples; $^qCS = 0$ when all samples are completely distinct, and

210   $^qCS = 1$ when all are identical. When $q = 0$, and $N = 2$, it equals the Jaccard index, and for $q = 2$

211   the Morisita-Horn-Index (Jost 2007).

212

213   **RESULTS**

214   We recorded a total of 506 vascular plant species from 85 families and 324 genera in the 37

215   lentic wetlands. 407 species were woody plants and 99 aquatic species. There were 411 (81%)

216   typical species of Meta Piedmont and of the remaining 95 introduced species (19%), 43

217   corresponded to introduced exotic species and 52 to native exotic ones. Additionally, some of the

218   species are categorized as threatened in red lists: *Cedrela odorata* as endangered in Colombia

219   and vulnerable (IUCN 2013), also the *Bactris gasipaes* and *Syagrus sancona* in the national

220   category as Vulnerable (VU A2ac).

221

222   **Completeness and diversity patterns**

223   The sampling coverage in each wetland was higher than 74%. Taking into account the wetlands

224   according to the type and origin, completeness was greater than 92% (Table S1). Given the high

225   inventory reliability, diversity comparisons were performed using the observed values.

226   There was a great variation in local diversity between wetlands in richness (^0D) and

227   dominant species (^2D) (Figures 2-3 and Tables S1-S2), being highest in the semi-natural lake

228   SNL6 (Lake Bioparque Ocarros, 94 species) and lowest in the constructed lake CL6 (Lake La

229   Tonga, 11 species, see Table S2). There were no statistical differences in the mean alpha

230   diversity ($\bar{\alpha}$) of woody and aquatic plants for both wetland type and origin (Figures 2-3 and

231   Table S3). Total alpha diversity (α) showed differences among wetland types for both woody and

232   aquatics plants (Figures 2-3 and Table S2). Woody species richness (^0D) was highest in FF (212

233   ± 12) and SNL (201 ± 13), and it was lowest in HC (78 ± 9) and RF (68 ± 6), presenting large

234   richness difference magnitude between FF and RF (212%) as well as between SNL and RF

235   (196%) (Fig 2a). The pattern was similar regarding dominant species (^2D), especially in HC,

236   which showed the highest inequality ($RLI_{0,2} = 0.52$) (Fig 2b and Table S1), being the most

237   dominant species *Mabea trianae* and *Bactris corossilla* with 29% and 16% of all individuals.

238   In aquatic plants there were also marked differences in total alpha diversity in the two

239   orders evaluated (^0D and ^2D), especially between SW and HC with a difference magnitude of

240   167% for species richness and 177% in terms of dominant species (Fig 2c). In general, the

241   inequality values were low. SNL was the wetland type with greater dominance ($RLI_{0,2} = 0.25$,

242   Fig 2d and S1 Table), where the presence of *Ludwigia inclinata,* with 16% of their plant

243   coverage, stands out.

244   With regard to wetland origin, woody plants in artificial wetlands had higher species

245   richness (^0D), mixed wetlands were more diverse regarding dominant species (^2D), and natural

246   wetlands were the least diverse (Fig 3a, b), but had more inequality ($RLI_{0,2} = 0.3$). Species

247   richness difference magnitude was 31% between artificial and natural wetlands, and dominant

248   species difference magnitude was 101% between mixed and natural wetlands. In aquatic plants,

249   the differences in diversity were low between origins (Fig 3c, d), as well as the values of

250   inequality ($RLI_{0,2} < 0.24$). However, natural wetlands had greater species richness (^0D) and 14

251   species were exclusive in these.

252

253   **Compositional similarity (^qCS)**

254 Compositional similarity in the whole landscape (i.e., for the entire set of wetlands studied) was

255 low, but it showed a high variability within wetland types (Table S4). For both plant formations

256 there was a high internal variability in the groups analyzed and ^{q}CS was lower within groups

257 than among groups (Fig 4a, b). Taking into account the diversity of woody plants, constructed

258 lakes (CL) were the wetland type with less similarity for all species ($^{0}CS = 0.07$), and heronries

259 (HC) for dominant species ($^{2}CS = 0.01$), while rice fields (RF) showed higher similarity, which

260 increased as q increased ($^{0}CS = 0.23$ to $^{2}CS = 0.38$, Fig 4a). The pattern was similar in aquatic

261 plants, it showed low similarity values, especially in CL and with maximum values in RF ($^{0}CS =$

262 0.08 and 0.32, respectively). All other wetland types had values lower than 0.17. Regarding

263 dominant species, SW showed the lowest and HC the highest values ($^{2}CS = 0.1$ and 0.26

264 respectively, Fig 4b). Comparing CS of wetland types in woody and aquatic plants, we found a

265 higher similarity among categories than within them in the two orders of similarity ($^{0,2}CS$)

266 (Figure 4a, b and Table S4).

267   Compositional similarity regarding the origin of wetlands in woody plants was low

268 within the categories (natural, mixed and artificial) and intermediate among them. Natural

269 wetlands had the highest similarity, especially in dominant species ($^{0}CS = 0.16$ and $^{2}CS = 0.27$)

270 (Fig 4c). In the same way, in aquatic plants the compositional similarity was low within each

271 origin category ($^{q}CS < 0.16$) and intermediate among them ($^{q}CS = 0.5$) for both richness (^{0}CS)

272 and dominant species (^{2}CS) (Fig 4d and see Table S4).

273

274 **DISCUSSION**

275 This is the first comparative study on the diversity of plants in freshwater inland wetlands under

276 different regimes of management in the Neotropical region. Although the total area of 37

277   wetlands studied (424 ha) and their forest area (435 ha) associated represent less than 1% of

278   wetland coverage in the Orinoco region and 1% of the Meta Piedmont tropical humid zonobiome

279   (Romero-Ruiz et al., 2004), our results indicated that these wetlands make a considerable

280   contribution to local and regional diversity of woody and aquatic plants. The diversity of plants

281   found represents around 55% of the woody species of the Meta Piedmont forest (Carvajal et al.,

282   2007), 12% of the flowering plants (Minorta-Cely & Rangel-Ch. 2014), and 29% of aquatic

283   plants (Fernández, Bedoya & Madriñán 2015) of the Colombian Orinoco river basin region.

284   Typical Piedmont species showed high representation (81%), but the portion of introduced plants

285   was considerable (19%), and had already an impact on diversity patterns and probably on the

286   function of wetlands (Hager 2004; Lambdon, Lloret & Hulme 2008). The high diversity of the

287   woody plants is related to forest of Meta Piedmont, where species of the Amazon and the Andes

288   region converge, in addition to species associated with the eastern savannas (Molano 1998;

289   Fernández et al., 2010), while aquatic plant diversity is related to the high complexity and variety

290   of aquatic ecosystems in the Orinoco region (Rial 2014; Fernández, Bedoya & Madriñán 2015).

291   Therefore, removal of these remnants of the landscape could endanger the conservation of plants

292   of a region characterized by its high biodiversity (Bates 1948; Hernández et al., 1992; Molano

293   1998; Fernández et al., 2010).

294   Contrary to our expectation, the origin of natural wetlands had low diversity both in

295   richness and dominant species. Which is associated to the fact that the heronries (HC) presented

296   the lowest diversity between wetland types. Probably due to the accumulation of guano caused

297   by the congregation of birds, which may have led to a naturally caused impoverishment of

298   diversity due to the high nitrogen content of excrements (Ayarzaguena, Pérez & Ramo 1981),

299   and it has been shown that a high bird activity can reduce the plant density of heronries (Weseloh

300   & Brown 1971). Additionally, they are strongly altered by livestock which modifies the structure

301   of the surrounding vegetation, since the increase of cattle grazing can affect negatively the

302   wetland diversity (Junk 1993). On the contrary, swamps (SW) did not have such a low diversity,

303   but lower than expected, as they are the most representative natural wetlands in the region (Lasso

304   et al., 2014). The diversity of these wetlands can be related to the persistent human intervention

305   along the time. Despite some swamps are locally protected, most of them are public lands, where

306   chronic extraction of timber and urbanization processes in surrounding areas have been common

307   (Machado, Rial & Lasso 2011).

308   The finding that artificial wetlands have a greater diversity of woody plants can be

309   explained by the fact that both fish farms (FF) and constructed lakes (CL) are created by private

310   enterprises, where owners have particular interests. Most of these wetlands were built on relict

311   forest. Meanwhile, mixed wetlands retain a high diversity of species typical of Piedmont because

312   they were developed on natural wetlands for recreational (semi-natural lakes - SNL) and

313   agricultural (rice fields - RF) purposes, and its management allows to keep a portion of the

314   diversity of native plants. The use of agrochemicals is often associated with the decline of plant

315   diversity (Rolon & Maltchik 2009); although RF belonged to the group with higher diversity, we

316   cannot exclude the possibility that without agrochemicals diversity would still be higher.

317   Our results show that the diversity patterns of plant species in and around wetlands are

318   the result of both the heterogeneity of these wetlands at the landscape scale and human activities

319   related with their management. Although wetlands are isolated systems, their heterogeneity and

320   diversity have been attributed largely to the interaction with adjacent terrestrial and other aquatic

321   ecosystems such as flooded and riparian forests (Mitsch & Gosselink 2015; Pott & Vila da Silva

322   2015), elements that contribute to connect and maintain diversity in human-dominated

323   landscapes as the Meta Piedmont (Molano 1998; Rangel-Ch 1998; Minorta-Cely & Rangel-Ch.

324   2014).

325   The results of this study support the importance of small forest fragments to conservation

326   in human-dominated landscapes (e.g., Flinn, Lechowicz & Waterway 2008; Arroyo-Rodríguez et

327   al., 2009). Despite the small size of the fragments of vegetation (<11 ha on average), the

328   diversity of plants found is astonishing. In highly modified landscapes, conservation and

329   management of a large number of small fragments can increase the differentiation in

330   composition and reduce the probabilities of extinction. Similar results were found by Arroyo-

331   Rodríguez et al., (2009) in Los Tuxtlas (Mexico), where even fragments less than 5 hectares

332   were of great value to the maintenance of regional diversity. Small patches can be used as

333   stepping stones that increase the landscape's connectivity and facilitate movements among

334   patches, and they may have complementary or supplementary resources that may favor survival

335   of many animal species in fragmented landscapes (e.g., Brotons, Mönkkönen & Martin 2003;

336   Pasinelli et al., 2008). Other authors have already highlighted the importance of small wetlands

337   to regional plant diversity (Richardson et al., 2015), not only of natural wetlands (Flinn,

338   Lechowicz & Waterway 2008) but also of small created wetlands (Chester & Robson 2013).

339   Therefore, maintaining a diverse set of created wetlands can mitigate the reduction of diversity

340   associated to natural wetlands loss, serving as shelter for birds and other organisms (e.g., Canals

341   et al., 2011; Hapner et al., 2011). Similarly, they can contribute to hydrological dynamics and

342   serve as areas for future ecological restoration (Moreno-Mateos et al., 2015).

343

344   **Species composition and future scenarios**

345   In our study compositional similarity was low (<0.5) compared to other studies in small

346   forest patches in human modified landscapes, where higher CS-values were related to

347   homogenization, and lower values to differentiation processes (See details in Arroyo-Rodríguez

348   et al., 2013). The low compositional similarity values found can be explained by differences in

349   type and origin of wetlands, being interesting that compositional similarity increased in most

350   cases by comparing the dominant species (i.e., of the most abundant species), which makes clear

351   the role of management of wetlands as a factor that determines taxonomic differentiation. We

352   found higher differences in species composition within the wetland categories than among them,

353   for both, origin and management. This pattern can be attributed to the high heterogeneity of

354   wetland conditions, maybe due to external ecological factors and different disturbance levels

355   (Clément & Proctor 2009). Other wetland diversity studies also reported high beta diversity

356   related to spatial heterogeneity (Flinn, Lechowicz & Waterway 2008; Neiff et al., 2011). This

357   could be attributed to the fact that in wetland remnants the habitat heterogeneity is the main

358   driver for species richness, besides other attributes as its size (Shi et al., 2010). The naturally

359   patchy distribution of wetlands also could contribute to a lower compositional similarity in these

360   ecosystems (Dornelas, Soykan & Ugland 2011),

361   An important component in the composition of species in these lentic wetlands was that

362   19% corresponded to introduced plant species, half of them are exotic species from outside of

363   Colombia, and 13 have invasive potential (Cárdenas, Castaño & Cárdenas 2010). Species

364   introduction in this region is the result of: 1) planting of ornamental species as shade trees,

365   flower beds and fruit trees for the embellishment predominantly of artificial and mixed wetlands

366   (SNL, CL and FF); 2) sowing of forage species for livestock and, 3) the introduction of aquatic

367   plants to decorate the lakes (CL) and for aquiculture uses (FF). Therefore, management of

368   wetlands determines the change of diversity with the introduction of exotic and native species.

369   As it is known, the introduction of alien species is considered a threat to biodiversity (Alvarado

370   & Gutiérrez 1997; Cárdenas, Castaño & Cárdenas 2010), and the ecological integrity of wetlands

371   (MMA 2002; Gallardo et al., 2015) is one of the major drivers of biotic homogenization (Chen et

372   al. 2010). That is why it requires the implementation of protocols for invasive species

373   management in the creation and maintenance of wetlands (e.g., gardens, landscaping, fences

374   living and restoration).

375   We suggest two opposed scenarios that may explain current plant diversity patterns in

376   these lentic wetlands and may potentially contribute to understanding future conservation

377   scenarios: 1) diversity is high because of the landscape heterogeneity, similar to the natural

378   diversity pattern before fragmentation, and patches are sufficiently connected in order to

379   maintain diversity in the long term and, 2) the low compositional similarity is a sign of

380   independent dynamics of the wetland communities, hence plant populations are not sufficiently

381   connected, increasing the probability that rare species may disappear from most wetlands

382   (Gutzwiller & Flather 2011). This could decrease both local and regional diversity.

383   Homogenization processes may cause local extinction of some species and lead to the dominance

384   of few others (McKinney & Lockwood 1999; Arroyo-Rodríguez et al., 2013).

385

386   **Management and conservation**

387   Our results suggest that created lentic wetlands (i.e., artificial and mixed) can have a key role in

388   plant diversity conservation by increasing the available habitat in the region for a variety of

389   typical species. Nevertheless, the plant diversity in natural wetlands may not be replaced or

390   equaled by artificial wetlands, yet the human-made wetlands are a way of safeguarding

391   biodiversity and partially compensate against rapid loss and transformation of natural wetlands

392   (Yoon 2009; Ghermandi et al., 2010). Created wetlands have the capacity to sustain biodiversity

393   or mitigate negative effects of wetland degradation (Galatowitsch & van der Valk 1996; Chester

394   & Robson 2013), but in some cases their high diversity is the product of more early-successional

395   stage species (Heaven, Gross & Gannon 2003).

396   Currently the Piedmont is a highly fragmented landscape (Romero-Ruiz et al., 2004;

397   Etter, McAlpine & Possingham 2008; Romero-Ruiz et al., 2009) and conservation strategies for

398   wetlands and forests have been reduced and inefficient. A new conservation model could be the

399   promotion of 'archipelago reserves' (Halffter 2007). This approach is particularly useful in

400   highly modified landscapes with high beta diversity, which could integrate the variability of the

401   landscape and allow the conservation of high heterogeneity and plant diversity found in the

402   region (Halffter 2005; 2007). Therefore, we strongly recommend including all wetland types into

403   conservation and management programs, considering how each of them is already contributing

404   to landscape diversity, and how some of them could be improved under appropriate management

405   goals. Also, we suggest the implementation of conservation and restoration strategies according

406   to the wetland type as well as the promotion of local policy for their regulation and management,

407   integrating wetland ecology (Mitsch & Gosselink 2015) and sustainable utilization, particularly

408   through promoting reconciliation between human land use and biodiversity from integration of

409   the different social actors (i.e., citizens, stakeholders, policy makers and scientists). All these

410   proposals are a way of safeguarding plant diversity of the Meta Piedmont forest species and the

411   lentic wetlands.

412

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417

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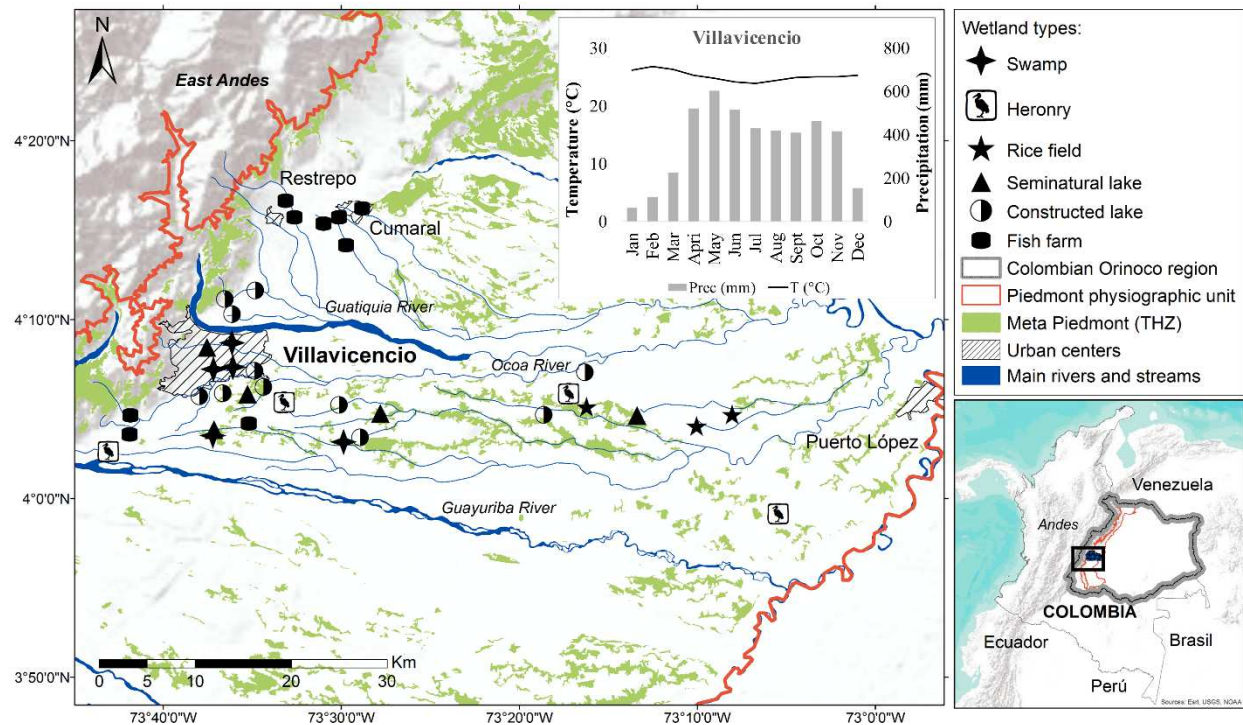597   109X.2009.01046.x

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625 **Tables**

626

627 **Table 1. Lentic wetlands studied.** Size refers to total area of water surface (424 ha) and forest

628 coverage (435 ha) in a 500m buffer calculated from centroid of each wetland. Mean ± SD shown

629 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)

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642 **Figures**

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645 The climograph shows the mean temperature (line) and precipitation (bars) of Villavicencio

646 municipality.

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648 **Fig 1. Localization of lentic wetlands at the Meta Piedmont in Colombian Andean-Orinoco**

649 **region.** Municipalities of Villavicencio, Restrepo, Cumaral and Puerto López with urban center.
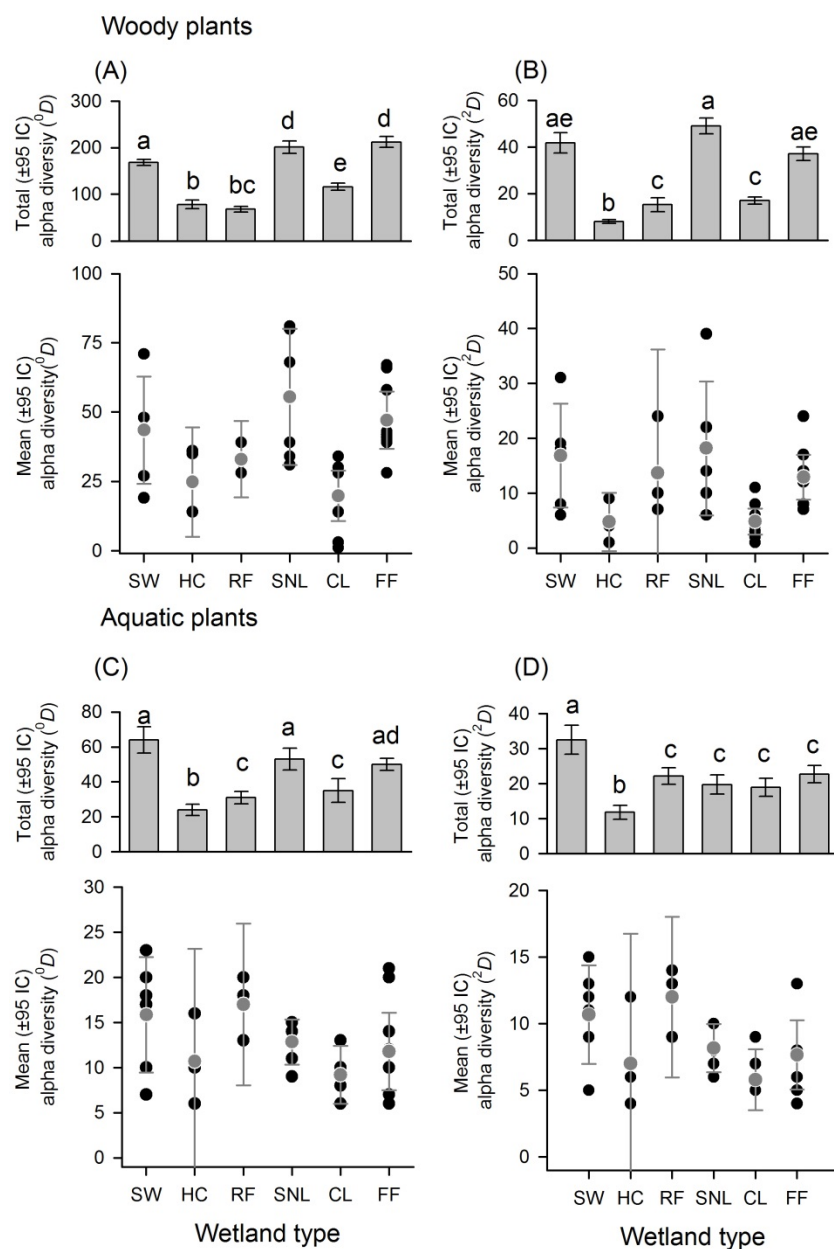
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Fig 2. Alpha diversity of woody and aquatic plants according to wetland types. Wetland

types: swamps (SW); heronries (HR); rice fields (RF); semi-natural lakes (SNL); constructed

lakes (CL); fish farms (FF). Diversity using Hill numbers: species richness (^0D) and dominant

species (^2D). 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
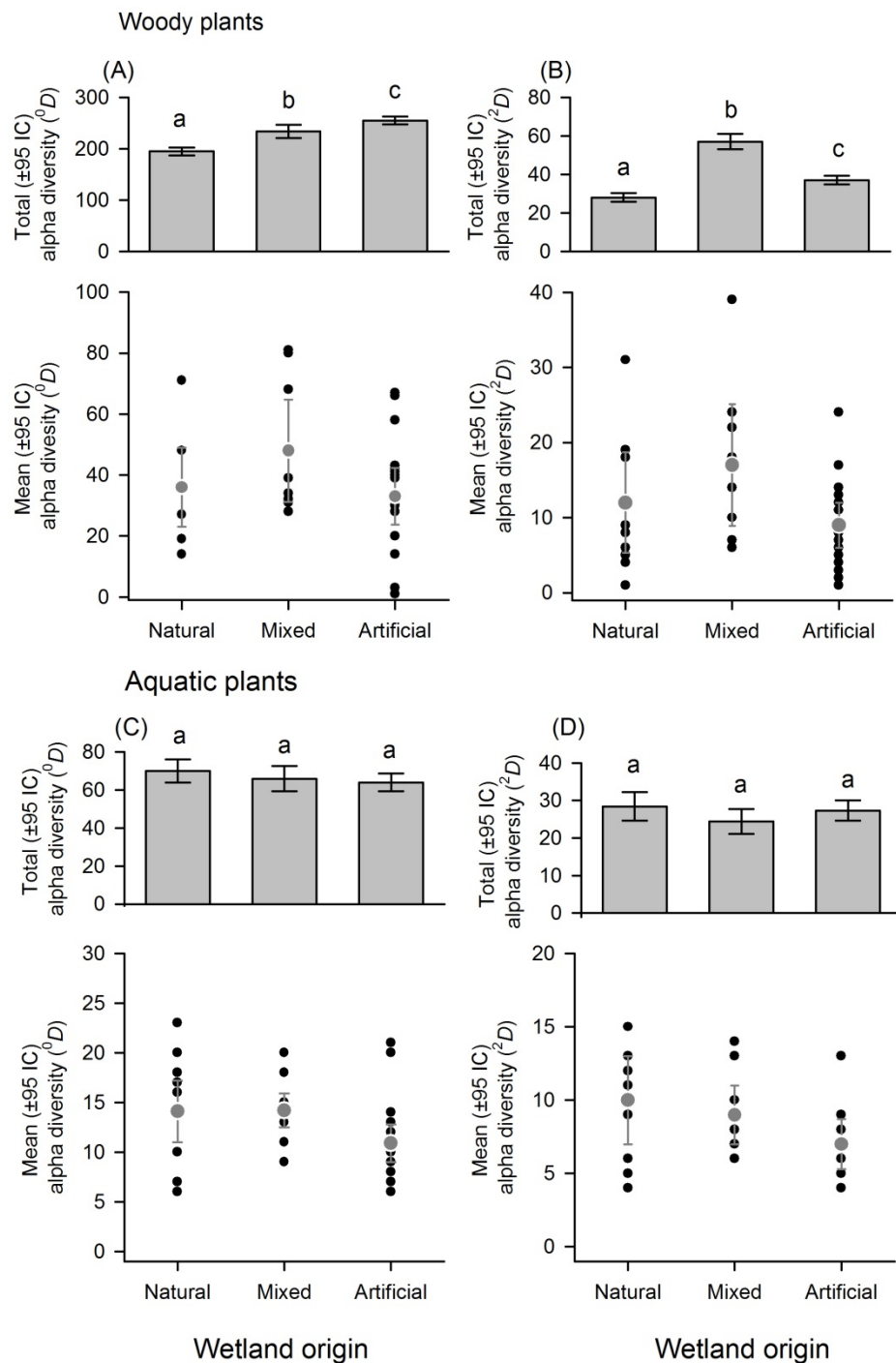
alpha diversity is different.

Fig 3. Alpha diversity of woody and aquatic plants within and among wetland origins.

Diversity using Hill numbers: species richness (^0D) and dominant species (^2D). Mean alpha

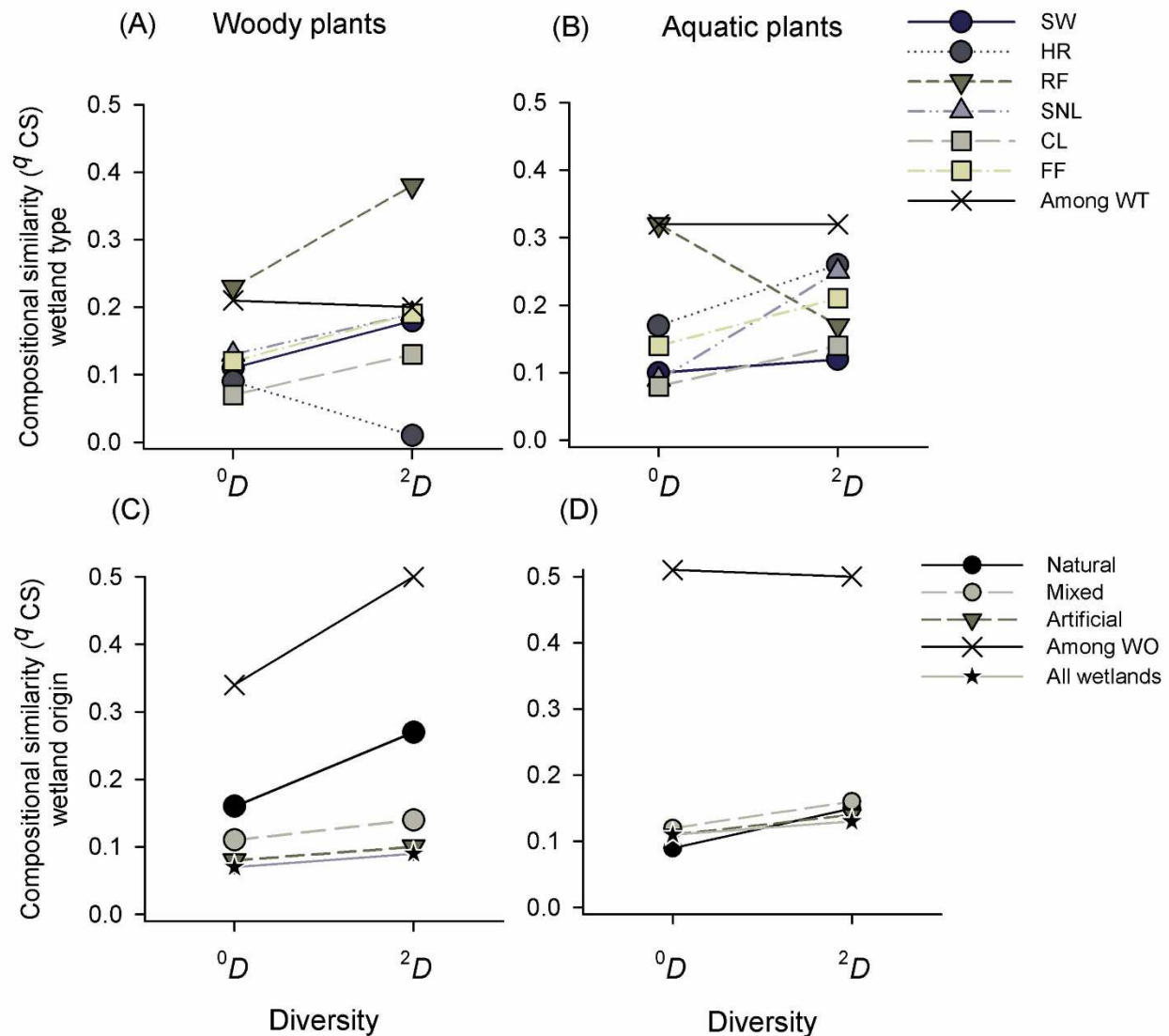diversity are gray points and local alpha diversity black points.

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).