Ecology and Evolution

Open Access

Regionally nested patterns of fish assemblages in floodplain lakes of the Magdalena river (Colombia)

Carlos Granado-Lorencio[1], Andrés Hernández Serna[2], Juan David Carvajal[2],
Luz Fernanda Jiménez-Segura[2], Alejandra Gulfo[2] & Frank Alvarez[2]

[1]Department of Plant Biology and Ecology, Faculty of Biology, University of Sevilla, Box 1095, 41080 Sevilla, Spain
[2]Ichthyology Group; Sciences Institute, University of Antioquia, Medellin, Colombia

Abstract

We investigated if fish assemblages in neotropical floodplain lakes (cienagas) exhibit nestedness, and thus offer support to the managers of natural resources of the area for their decision making. The location was floodplain lakes of the middle section of the Magdalena river, Colombia. We applied the nested subset analysis for the series of 30 cienagas (27 connected to the main river and three isolated). All fish were identified taxonomically in the field and the matrix for presence–absence in all the lakes was used for the study of the pattern of nestedness. The most diverse order was Characiformes (20 species), followed by Siluriformes (19 species). Characidae and Loricaridae were the richest families. The species found in all the lakes studied were migratory species (17), and sedentary species (33). Two species (*Caquetaia kraussii* and *Cyphocharax magdalenae*) were widespread across the cienagas archipelago (100% of incidence). Nestedness analysis showed that the distribution of species over the spatial gradient studied (840 km) is significantly nested. The cienagas deemed the most hospitable were Simiti, El Llanito, and Canaletal. Roughly, 13 out of the 50 species caught show markedly idiosyncratic distributions. The resulting dataset showed a strong pattern of nestedness in the distribution of Magdalenese fishes, and differed significantly from random species assemblages. Out of all the measurements taken in the cienagas, only the size (*area*) and local richness are significantly related to the range of order of nested subset patterns ($r = -0.59$ and -0.90, respectively, at $p < 0.01$). Differential species extinction is suggested as the cause of a nested species assemblage, when the reorganized matrix of species occurring in habitat islands is correlated with the island area. Our results are consistent with this hypothesis.

Introduction

Biodiversity varies throughout the range of environmental gradients (landscape), with variations in the richness of species; some areas are rich, whereas others are poor (Watts 1996). Even if there has not been much interest in the study of these types of patterns at a regional or local level, two alternative paradigms have been proposed to explain local community assembly: dispersal-driven assembly ("*island paradigm*") and niche assembly ("*trait-environment paradigm*") (Hubbel 2001).

Numerous studies have revealed that variations in species assemblages can reflect nested distribution patterns at the landscape level. Nestedness in metacommunities is demonstrated when the assemblages of species-poor sites are subsets of those in the successively richer assemblages (Atmar and Paterson 1993; Baker and Patterson 2011). The concept of nestedness refers more to a description of an observable situation than an ecological process, which is why it can be considered as a measurement of the ordered composition of biodiversity, in a determined geographical area. In any case, there is no consensus concerning the mechanisms which determine nestedness in nature (Higgins et al. 2005).

The Magdalena basin supports a richness comprising 213 fish species (Maldonado-Ocampo et al. 2008) and includes the most productive fishing areas in Colombia. However, at the present time, the floodplain is undergoing dramatic transformation and deterioration of habitats,

caused by the expansion of agriculture, cattle, gold mining, oil extraction, African palm cultivation, and illicit cocaine plantations. The fishing population is estimated at 35,000 people, with an annual catch of less than 17,000 t year^{-1} (a sixth part of that caught 30 years ago). As a greater part of the fishes are obtained from the flooded ciénagas, these are overexploited owing to the great number of fishermen who have no other means for survival. Along the river channel, the fishermen's catches are concentrated during five months, the three months during the first season of the year (December–February) and lastly, in the second season (July–August), taking advantage of species migration. Traditionally, the commercial catches include three species: *Prochilodus magdalenae* Steindachner, 1879 (bocachico), *Pseudoplatystoma magdaleniatum* Buitrago-Suárez and Burr 2007 (pintadillo), and *Pimelodus blochii* Valenciennes 1840 (blanquillo) (Galvis and Mojica 2004), but the decline in catches has caused fishing pressure to fall on species of smaller size, with diminished fertility. Out of the 44 species "in danger" included in the Red Book of Fish from Colombia, which are in the endangered category, 19 are from the Magdalena River Valley. Two of these which are important to fisherman are in the category of Critically Endangered (*Prochilodus magdalenae* and *Pseudoplatystoma magdaleniatum*), three are Endangered (*Ageneiosus pardalis*, *Ichthyoelephas longirostris*, and *Sorubim cuspicaudus*), eight are Vulnerable, and six are Near Threatened (Mojica et al. 2002).

In order that the conservation of an elevated number of species in a region should be effective, the first stage requires a knowledge of the distribution of species, the patterns of richness, and taxonomic composition, as well as their interrelationships through space and time (Margules and Pressey 2000; Sachs et al. 2009). For this purpose, methodologies should be applied which offer the greatest reliability in terms of their results and applicability. Among the few possible alternatives which fulfill these requisites is that of measuring *biogeographic nestedness* (Patterson and Atmar 1986; Patterson 1987; Atmar and Patterson 1993). It is within this framework of reference that the present study has been carried out; in a geographical area which brings an elevated biodiversity of fish, with many endemic species in the hydrographic basin, and an ever more numerous fisherman population, caused by displacement from other zones of the country because of armed conflict and where fishing constitutes the only means of susbsistence.

Methods

The middle section of the Magdalena River Valley constitutes an extensive floodplain with many lakes (cienagas) marginal to the main channel, covering an estimated area of 22,000 km^2 (Correa 2008). The seasonality of the flood-
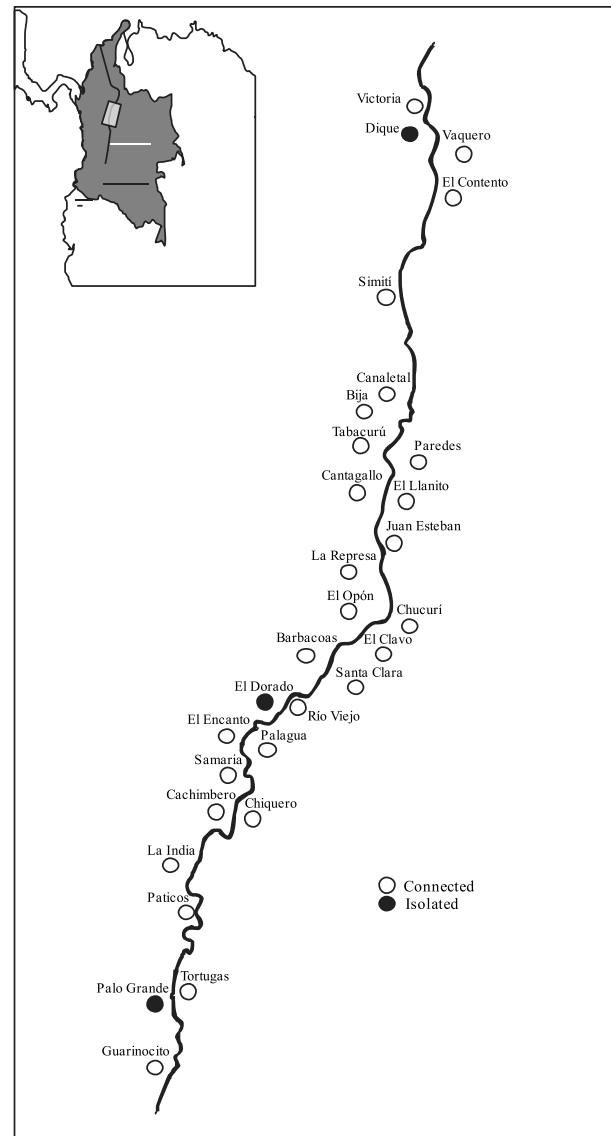

Figure 1. Location of the floodplain lakes used in the analyses of nested subsets for fish species in Magdalena river.

ing manifests highly predictable timing, permitting the evolution of adaptive life strategies for the species (Restrepo and Jerfve 2000). The fish undertake two kinds of migrations: *longitudinal*, along the principal water channel of the river and *lateral*, between the river channel and the floodplain.

Thirty cienagas of various sizes were selected for sampling along 840 km of the midsection of the Magdalena river floodplain between the localities of Puerto Boyacá and Barrancabermeja (27 connected to the main river and three isolated; Fig. 1 and Table 1). Samples were taken during the high water season (November). The sampling program began in 2008 (10 cienagas) up to 2010 (20 cienagas). The sampling

Table 1. Name, geographic area, main river, and hydrological and limnological characteristics of floodplain lakes studied in the Magdalena basin.

Name	Latitude	Longitude	Main river	Area (Has)	Average depth (m)	Average pH	Avenge conductivity (μS)	Richness	Distance of the main river (m)
Guarinocito	05°20′25.1″N	74°44′04,l″W	Magdalena	49	8.1	6.98	138.38	24	1140
Tortugas	05°45′32.54″N	74°40′46.34″W	Magdalena	5	3.7	5.04	54.91	9	1000
Paticos	06°2′14.19″N	74°38′6.82″W	Cocoma	4	1.5	4.49	4339	13	98
Palagua	06°04′07.2″N	74°31′20.7″W	Magdalena	192	1.6	7.08	70.41	16	18,000
La India	06″09.605′N	74°37.808″W	Nare	138	1.1	5.59	74.05	27	10,290
Chiquero	06°22′54.2″N	74°27′36.5″W	Magdalena	62	2.3	6.37	46.83	20	2284
Samaria	06°30′03.3″N	74°25′19.8″W	Magdalena	24	1.3	6.9	55.75	15	6650
Cachimbero	06°21′31.6″N	74°22′ 48.0″W	Magdalena	387	2.7	6.56	46.40	22	6850
El Encanto	06°27′37.1″N	74°21′50.6″W	Magdalena	31	3.0	6.97	4735	16	6350
Santa Clara	06°39′24.2″N	74°19′08.2″W	Magdalena	127	1.7	6.56	26.27	30	2770
Río Viejo	06°34′43.8″N	74°17′33.5″W	Magdalena	502	2.2	6.75	45.15	27	6890
El Clavo	06°45′34.6″N	74°05′20.7″W	Carare	64	2.1	5.75	9.06	19	2015
Barbacoas	06°44′18.6″N	74°15′24.4″W	Magdalena	1158	2.1	6.95	57.92	26	6190
Chucuri	06°50′10.3″N	74°36′36.0″W	Magdalena	1247	1.8	7.1	45.45	27	3560
El Opón	06°54′46.5″N	73°53′54.2″W	Magdalena	1095	2.3	6.85	43.28	26	7414
Juan Esteban	07° 01′33,4″ N	73°50′54,1″W	Magdalena	71	2.5	6.97	107.62	17	3080
La Represa	07°59′08.2″N	73°55′10.9″W	Magdalena	35	2.9	6.83	9537	15	1000
El Llanito	07°9′34.4″N	73°51′04.0″W	Sogamoso	1019	2.3	7.11	6830	31	9299
Paredes	07°26′85.6N	73°45′823W	Lebrija	881	2.5	6.18	13.91	26	41,090
Tabacurú	07°28′25.9″N	73°56′52.7″W	Magdalena	125	3.9	6.49	90.75	27	680
Bija	07°26′39.4″N	73°57′45.4″W	Magdalena	211	6.1	6.9	79.43	24	1210
Cantagallo	07°23′19.9″N	73°55′00.3″W	Magdalena	440	1.4	7.12	84.94	27	5
Canaletal	07°31′13.7″N	73°55′02.7″W	Magdalena	1259	2.0	8.09	117.62	29	854
Simití	07°59′29.9″N	73°55′40.0″W	Magdalena	2333	2.7	8.55	63.46	39	3694
Vaquero	08°19′21.9″N	73°44′03.1″W	Magdalena	116	2.5	9.08	119.50	30	2614
El Contento	08°13′29.6″N	73°45′34.7″W	Magdalena	148	1.9	7.63	104.00	27	6847
La Victoria	08°28′09.1″N	73°46′45.8″W	Magdalena	1597	1.8	9.92	186.70	21	4064

method was the same for all the lakes. Fish were caught using experimental multifilament gillnets (100 × 3 m), with mesh sizes from two to 10 cm between opposite knots, and the order of the panels was originally random (Kukilahti et al. 2002; Robertson et al. 2008). Besides, these kinds of nets are easy to use, low in cost, and appropriate for varying profundities and depths (Winemiller et al. 2000).

Nets remained set for 24 h and were checked every four hours. In all lakes, fishes were collected within structurally different aquatic habitats: *littoral with trees, littoral without trees, pelagic,* and *the connecting channel between cienaga and canal.* In all analyses for a lake, only the taxa present at that lake were used. We refer to the number of species present at a lake as the *local species richness* at that lake.

In each habitat, measurements of depth, pH, and conductivity (μS) were taken. The measurements for environmental variables were analyzed using a one-way ANOVA with the aim of discovering differences between habitats (Bonferoni correction included). Pearson's correlation analysis was used to explore the possible correlations between the environmental variables measured. For each cienaga, the area was calculated. We use the length of the channel that links the cienaga to the

main river as a measurement of connectivity (Tockner et al. 1999).

The matrix for presence–absence in all the cienagas was used for the study of the pattern of nestedness. Various systems have been proposed for measuring the adjustment of a determined matrix of presence–absence to the nested subset model: *N* (Patterson and Atmar 1986), *T* (Atmar and Patterson 1993), *U* (Cutler 1991), and *C* (Wright and Reeves 1992). The most popular measuring device is that of the matrix temperature *T*, introduced by Atmar and Patterson (1993)**,** with its recent modifications (Rodriguez-Gironés and Santamaria 2006; Ulrich and Gotelli 2007; Ulrich et al. 2009). NEST-CALC software was used to sort the dataset from high to low for site diversity (top to bottom) and species diversity (left to right); in our case, the cienagas represent the rows and the species the columns. NESTCALC also calculates as statistical test value *T* of the order (nestedness) or disorder (lack of nestedness) in the dataset (Atmar and Patterson 1993). *T* ranges from 0 to 100°. A temperature near to 0° (complete order) would indicate a very nested matrix, whereas one near to 100° (complete disorder) would not be nested, but random. The observed *T* value was then compared to a distribution of

Table 2. Some characteristics of the three metrics for biogeographic temperature obtained in this study: Nestedness Calculator, Bhmatnest, and Anhidado.

| | Nestedness Calculator | | BINMATNEST | | | ANHIDADO | |
			First	Second		T(Er)	T(Ce)
$T*$	17.36	15.7			17.36		
$p < T$	2.93×10^{55}		0.0000	*0.0000*		0.0000	0.0000
Average $T°$	70.47		71.00	35.40		72.99	50.99
Variante	2.9600		7.6400	3.7713			

values generated by Monte Carlo simulations. Every program was run 1,000 times to generate 1,000 random fish assemblages. NESTCALC was then used to calculate idiosyncratic T values by sites and by species presence or absence leading to specifically higher T values than the complete dataset. Such elevated T values may indicate that the species (or sites) in question was influenced by a biogeographic event different from that affecting the other species (or sites). Nested sites are those dominated by nested species and idiosyncratic sites are those with a majority of idiosyncratic species (McAbendroth et al. 2005). Idiosyncratic distributions are frequently generated by postisolation immigration (Cutler 1991).

To analyze nested structure among floodplain fish species, we utilized BINMATNEST, an implementation of Atmar and Patterson's (1993) temperature concept and metric, T, with an improved algorithm for packing matrices (Rodriguez-Gironés and Santamaria 2006). We used BINMATNEST to assess the significance of T in the observed matrices against three null hypotheses, each used to construct a pool of 1,000 simulated assemblage sets with the observed. The detection of nestedness is strongly determined by the metric and null models used (Heino et al. 2009). And this is the most controversial aspect of these types of methodologies. We also use the ANINHADO software designed by Guimaraes and Guimaraes (2006), which is based on the algorithms from the Nestedness Temperature Calculator. It is considered to be the best software package and permits choosing between four different null models.

In order to determine the correlations of nestedness, we used Spearman rank and partial Spearman rank correlation tests to find the order of the cienagas in the maximally packed matrix to cienaga area, measured environmental variables, and isolation ranks (Cutler 1994).

To estimate the minimum protected area, we constructed species–area model and cumulated by progressively adding the number of new species gained with each increase in lake area. For each model, three kinds of submodels were tested as linear regression (S/A), semilog model ($S/\log A$), and power model ($\log S/\log A$). The optimum models were determined to estimate the minimum protected areas for the total fish

species. Data analyses were conducted with STATISTICA 8.0 and EXCEL 2007.

Results

During the study, a total of 18,237 specimens, distributed among 50 species in 43 genera, 19 families, and six orders, were collected in the 30 lakes. The richness varied depending on the cienaga. Cienagas ranged in surface area between four (Paticos) and 2.333 Has (Simiti), and contained from nine (Tortugas) to 39 species (Simiti) from a total species pool of 50. Two species (*Caquetaia kraussii*, and *Cyphocharax magdalenae*) were widespread across the cienagas archipelago (100% of incidence), while eight species (*Colossoma macropomum, Geophagus steindachneri, Leporellus vittatus, Pseudopimelodus buffonius, Spatuloricaria gymnogaster, Sturisoma panamense, Sturisomatichthy leitoni,* and *Symbranchus marmoratus*) were restricted to a single cienaga each. Species with wide distributions comprised the poor assemblages, while richer assemblages contained these species plus a number of additional, more narrowly distributed forms.

The resulting dataset showed a strong pattern of nestedness in the distribution of magdalenese fishes, and differed significantly from random species assemblages generated using Monte Carlo simulations. The reorganized matrix obtained after the original data matrix was maximally nested. The calculated temperature of the whole cienagas was 17.36°. The expected temperature for the same fish assemblages was 70.47° (SD = 2.96°). Therefore, the probability of randomly obtaining a matrix colder than the one estimated was 2.31×10^{-55}. We detected a high degree of nestedness for the entire fauna under the BINMATNEST and ANHIDADO algorithms (Table 2). The results differ according to kind of cienagas: only connected ($T° = 20.59°$, fill 41.4%, $p\ T < 20.59° = 9.33 \times 10^{-48}$); only connected and native fish species ($T° = 21.15°$, fill 45.1%, $p\ T < 21.15° = 1.71 \times 10^{-41}$); only sedentary fish species ($T° = 20.81°$, fill 39.4%, $p\ T < 20.81° = 1.27 \times 10^{-27}$); all statistically significant and as such not random (null hypothesis).
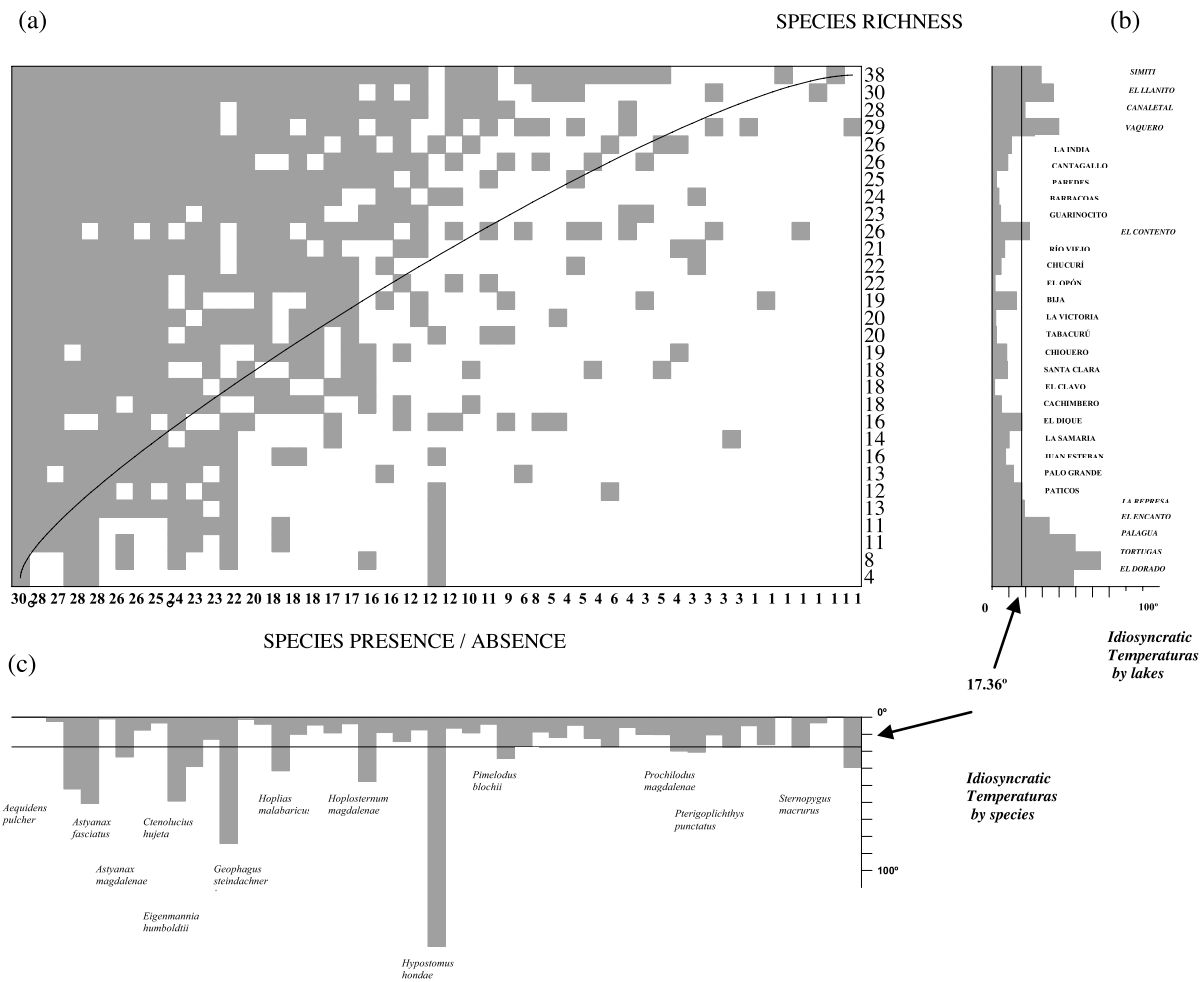
Figure 2. Maximally ordered species presence–absence matrix for 30 floodplain lakes in the Magdalena river, (a) packed matrix showing distribution of species (columns) and floodplain lakes (rows), (b) nested and idiosyncratic lakes ordered with corresponding species richness shown in, (c) idiosyncratic species are listed here, whereas all species collected are indicated in Table 3.

The first positions in the nesting range, both for the cienagas and species, are shown in Figure 2. The temperature method of Atmar and Patterson (1993) asserts that the topmost "cienaga" in a packed matrix is the most hospitable, while the leftmost species is most resistant to extinction. The cienagas deemed the most hospitable were Simití, El Llanito, and Canaletal. Probabilities of generating equally structured assemblages by chance were effectively zero. Spearman rank correlations between species order in the "maximally nested matrix "correlated significantly with its% incidence ($rs = -0.97$; $p \leq 0.001$), total abundance ($rs = -0.59$; $p \leq 0.01$). Out of all the measurements taken in the cienagas, only the size (*area*) and local richness are significantly related to the range of order of nested subset patterns ($r = -0.59$ and -0.90, respectively, at $p < 0.01$). In the same way, significant relationships are revealed if the analysis is carried out

with respect to the richness of migratory species ($r = -0.71$, $p < 0.05$) and sedentary species ($r = -0.77$, $p < 0.01$). The other variables (including connectivity) did not manifest any significance, some of them having strong relationships between each other. In our study, lake area was shown to be a factor significantly correlated with species richness ($r = 0.68$, $p < 0.01$).

Roughly 13 out of the 50 species caught (Table 3) show markedly idiosyncratic distributions (migrants species: *Astyanax fasciatus, Astyanax magdalenaea, Pimelodus blochii,* and *Prochilodus magdalenae;* sedentary species: *Ctenolucius hujeta, Eigenmania humboldti, Geophagus steindachneri, Hoplias malabaricus, Hoplosternum magdalenae, Hypostomus hondae, Sternopygus macrurus, Pterigoplichthys punctatus,* and *Trichogaster pectoralis*). La India and Simití supported the greatest number of idiosyncratic ichtyofauna (10 species).

Table 3. Fish species ordination in the "maximum parking" matrix. Names in boldface represent migratory fish species.

Rank		Rank		Rank	
1	*Caquetaia kraussii*	18	*Potamotrygon magdalenae*	35	***Brycon moorei***
2	***Cyphocharax magdalenae***	19	*Hypostomus tenuicauda*	36	*Oerochromis niloticus*
3	***Pimelodus blochii***	20	*Ageneiosus pardalis*	37	***Brycon henni***
4	*Trachelyopterus insignis*	21	*Gilbertolus alatus*	38	***Ichthyoelephas longirostris***
5	***Astyanax magdalenae***	22	*Sternoygus aequilabiatus*	39	*Pterigoplichtys punctatus*
6	***Prochilodus magdalenae***	23	***Cynopothamus magdalenae***	40	***Astyanax fasciatus***
7	*Roeboides dayi*	24	***Sorubim cuspicaudus***	41	*Sternopygus macrurus*
8	*Ctenolucius hujeta*	25	***Pseudoplatystoma magdaleniatum***	42	*Apteronotus mariae*
9	***Triportheus magdalenae***	26	*Hoplosternum magdalenae*	43	*Symbranchus marmoratus*
10	***Curimata mivartii***	27	*Plagioscion surinamensis*	44	*Spatuloricaria gymnogaster*
11	*Hoplias malabaricus*	28	*Pterigoplichtys undecimalis*	45	*Leporellus vittatus*
12	*Eigenmannia humboldti*	29	***Salminus affinis***	46	*Colossoma macrapomum*
13	***Leporinus muyscorum***	30	*Trichogaster pectoralis*	47	*Sturisomatichthy leightoni*
14	*Aequidens pulcher*	31	***Pimelodus grosskopfii***	48	*Pseudopimelodus buffonius*
15	*Dasyloricaria filamentosa*	32	*Eigenmannia virescens*	49	*Geophagus steindachneri*
16	*Centrochir crocodilii*	33	*Crossoloricaria variegata*	50	*Sturisoma panamense*
17	*Hypostomus hondae*	34	*Abramites eques*		

El Encanto, Samaria, El Dorado, and Opón revealed only three idiosyncratic species. It is important to emphasize that Palo Grande and Victoria suffer from very little fishing activity; El Dique, Simití, El Llanito, and Palagua suffer very high fishing and intensity of human activities (cattle and urban contamination, principally).

Discussion

Great differences exist between the natural systems where nestedness has traditionally been studied (e.g. landbridge islands, oceanic islands, and isolated mountains) and aquatic ecosystems, streams, and lagoons. Whereas the first group is characterized by the space and time scales which govern ecological processes, the last are very dynamic systems with high interconnectivity, dependent on the variations in the hydrological regimes (flooding) and other environmental factors dependent on seasonal and annual cycles (Godoy et al. 1999; Taylor and Warren 2001).

Nestedness is an important compositional descriptor that can potentially identify risk-prone species or groups of species. Due to the high correlation found between the nested structure and floodplain area, it is possible to predict the species composition on the basis of the cienaga area. In addition, the nested assemblage of some cienagas allows the identification of species at risk of total extinction should habitat area be reduced below that needed by the species. Also, certain rare species might be indicators of total species richness, because they would typically occur only in species-rich communities. Nestedness analysis is often portrayed as a tool to predict the order in which extinctions are likely to occur at a suite of sites in response to habitat reduction or other types of disturbance (Kerr et al. 2000).

Differential species extinction and differential species colonization have been proposed as the two main causes producing a nested species assemblage in habitat islands: (1) Differential species colonization is suggested when the reorganized matrix is correlated with some index of isolation (or connectivity) of the habitat islands, or with the dispersal ability of the species (Cook and Quin, 1995; Conroy et al. 1999). The species with greater capacity for dispersal are able to cover long distances, and colonize more distant sites, than those which are either less mobile or sedentary. This pattern has been observed in freshwater ecosystems (Taylor and Warren, 2001). Even if the connectivity (distance) to the main channel can be considered a prediction variable, this indicates the richness of a cienaga, or at least in relation to migratory species as has been demonstrated in certain Amazon floodplain lakes (Granado-Lorencio et al. 2005); in our study, it has not been possible to demonstrate this. This may be because of the varying hydrological behavior of the river, or the different capacity for a species to colonize or simply that the range of lengths of the connecting canals was not sufficient. (2) Differential species extinction is suggested as the cause of a nested species assemblage, when the reorganized matrix of species occurring in habitat islands is correlated with island area (Soulé et al. 1992). Our results are consistent with this hypothesis.

The range of nestedness in the cienagas did not manifest significant relationships with the environmental variables, except in terms of the size of the cienaga (log area). However, other unevaluated factors may also affect this: habitat nestedness (Wright et al. 1998). If the diversity of habitat is not uniform between cienagas, or even in the same cienaga throughout the year (*habitat selection* hypothesis; Rodríguez and Lewis 1990), it may allow a greater number of species to

coexist than others, producing a nested pattern. (It would also be possible if some disturbance factor did not affect all the cienagas equally; e.g., contamination and intensity of fishing.) The most conserved cienagas are Simiti and El Llanito, besides being those which suffer from least fishing pressure. On the other hand, El Dorado, Tortugas, El Encanto, and Represa are those which show greatest environmental deterioration from anthropic causes such as cattle, being situated in oil extraction zones, loss of vegetation cover on the banks, and the effect of urban contamination isolated from the main river.

Idiosyncratic site temperatures are not usually independent of the idiosyncratic species temperature; assemblages dominated by idiosyncratic species usually have a high local species turnover (Soinen 2008). McAbendroth et al. (2005) indicate that the idiosyncratic species occupy fewer sites than the nested species, this may indicate that the idiosyncratic species have less capacity for dispersal than the nested ones. In our study, the four most abundant species (*Cyphocharax magdalenae, Caquetaia kraussi, Trachelyopterus insignis*, and *Roeboides dayi*) are present in more than 86% of cienagas studied and none are idiosyncratic; however, only the first one of these are migratory species. Out of all the idiosyncratic species, four are migratory (*Astyanax fasciatus, Astyanax magdalenae, Pimelodus blochii*, and *Prochilodus magdalenae*) and the rest (10) have a sedentary lifestyle. This admits the possibility that species-specific, nonbiological factors exist, for example, pressure from fishing. Ten idiosyncratic migratory species suffer from intense pressure from fishing (*Ageneiosus pardalis, Curimata mivarti, Hypostomus hondae, Leporinus muyscorum, Pimelodus blochii, Pimelodus grosskopfii, Plagioscium surinamensis, Prochilodus magdalenae, Sorubim cuspicaudus*, and *Triportheus magdalenae*).

The analysis of nested subset structure in ecological communities has been linked to the debate surrounding refuge design: SLOSS (single large or several small reserves). In a low-temperature matrix, where species presence is predictable, the decision tilts in favor of the single large reserve. However, in a moderately warm matrix, species presence is relatively uncertain. Therefore, a number of species–island combinations exist for a given temperature, favoring several small reserves. The hot matrices are indicative of relatively quick local extinctions and highly probable resettlements.

Species–area relationships were usually applied in terrestrial reserve design (e.g. Lomolino et al. 2000). The approach is also applicable in floodplain lakes. It needs only two simple parameters (species richness and the size of area). A fundamental pattern is the way in which the total number of species increases as the sampled area increases. The increase in number of species comes about for two reasons: First, as more individuals are sampled, the chance of encountering additional species increases, especially if species are not randomly distributed. Second, a larger area is likely to be more environmentally heterogeneous, thus containing additional species that differ in their niches. More extensive areas comprise greater habitat diversity than other smaller ones (Gaston and Blackburn 2000), and in nested systems, small cienagas contain species with ample distribution and abundance (Patterson 1987).

The existing regional richness in Magdalena river (50 fish species) is contributed mainly by eight cienagas: Simiti, Vaquero, La India, El Llanito, Canaletal, Contento, Chucurí, and Samaria (6.284 Has). On the other hand, the minimum protected area of cienagas was estimated to be 2.800 Has. Dealing with the conservation of total fish fauna, we recommend that at least 2.800 Has of cienagas should be preserved (30, 3% of the total area studied). They could be regarded as "hotspots" while considering fish diversity conservation in the cienagas because they maintain rich assemblages. We propose that commercial fishing in the cienagas of the middle Magdalena river should be banned all the year round, and a core protected area, where all human activities are forbidden, should be demarcated.

Conservation planning and policy often demand that decisions about the fates of specific species and communities be made on the basis of a limited amount of information, gathered in a limited amount of time. The use of nested subset analysis of species occurrence patterns has become an increasingly common tool in community ecology and many have advocated its use in conservation planning, particularly in reserve design and predicting species susceptibility to extinction. These regularities obtained in our study permit introducing ecological aspects into the communities in these world regions for purposes of development and planning strategies for the conservation of biodiversity (Lomolino 2000).

Acknowledgments

References

Atmar, W., and B. D. Patterson. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–380.

Baker, M. A., and B. D. Patterson. 2011. Patterns in the local assembly of Egyptian rodent faunas: co-occurrence and nestedness. J. Arid Environ. 75:14–19.

Conroy, C. J., J. R. Demboski, and J. A. Cook. 1999. Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. J. Biogeogr. 26:343–352.

Cook, R. R., and J. F. Quin. 1995. The influence of colonization in nested species subsets. Oecologia 102:413–424.

Correa, S. B. 2008. Fish assemblage's structure is consistent through an annual hydrological cycle in habitats of a floodplain-lake in the Colombian Amazon. Neotrop. Ichthyol. 6:257–266.

Cutler, A. H. 1991. Nested faunas and extinction in fragmented habitats. Conserv. Biol. 5:496–505.

Cutler, A. H. 1994. Nested biotas and biological conservation. Metrics, mechanisms, and meaning of nestedness. Land. Urban Plan. 28:73–82.

Galvis, G., and J. I. Mojica. 2004. The Magdalena river fresh water fishes and fisheries. Aquat. Ecosyst. Health Manage. 10:127–139.

Gaston, K. J., and T. M. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford, U.K.

Godoy, J. R., G. Petts, and J. Salo. 1999. Riparian flooded forest of the Orinoco and Amazon basins: a comparative review. Biodivers. Conserv. 8:551–586.

Granado-Lorencio, C., C. R. Araujo, M. Lima, and J. Lobón-Cerviá. 2005. Abundance–distribution relationships in fish assembly of the Amazonas floodplain lakes. Ecography 28:515–520.

Guimaraes, P. R., and P. Guimaraes. 2006. Improving the analyses of nestedness for large sets of matrices. Environ. Model. Softw. 21:1512–1513.

Heino, J., H. Mykrä, and T. Muotka. 2009. Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. Divers. Distrib. 15:198–206.

Higgins, J. V., M. T. Bryer, M. L. Khoury, and T. H. Fitzhugh. 2005. A freshwater classification approach for biodiversity conservation planning. Conserv. Biol. 19:432–445.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton Univ. Press, Princeton, NJ.

Kerr, J. T., A. Sugar, and L. Parker. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. Conserv. Biol. 14:1726–1734.

Kurkilahti, M., M. Appelberg, T. Hesthagen, and M. Rask. 2002. Effect of fish shape on gillnet selectivity. A study with Fulton's condition factor. Fishery Res. 54:153–170.

Lomolino, M. V. 2000. Ecology's most general, yet protean pattern: the species–area relationship. J. Biogeogr. 27:17–26.

Maldonado-Ocampo, J. A., R. P. Vari, and J. S. Usma. 2008. Check list of the freshwater fishes of Colombia. Biota Colombiana 9:143–237.

Margulles, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

McAbendroth, L., A. Foggo, S. D. Rundle, and D. T. Bilton. 2005. Unravelling nestedness and spatial pattern in pond assemblages. J. Anim. Ecol. 74:41–49.

Mójica, J. I., C. Castellanos, S. Usma, and R. Alvarez, eds., 2002. Libro Rojo de las especies de peces dulceacuícolas de Colombia. Ministerio de Medio Ambiente, Bogotá, Colombia.

Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. Conserv. Biol. 1:323–334.

Patterson, B. D., and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biol. J. Linnean Soc. 28:65–68.

Restrepo, J. D., and B. Jerfve. 2000. Magdalena river: interannual variability (1975–1995) and revised water discharge and sediment load estimates. J. Hydrol. 235:137–149.

Robertson, C. R., S. C. Zeug, and K. O. Winemiller. 2008. Associations between hydrological connectivity and resource partitioning among sympatric gar species (Lepisosteidae) in a Texas river and associated oxbows. Ecol. Freshwater Fish 17:119–129.

Rodriguez, M. A., and W. M. Lewis, Jr. 1990. Diversity and species composition of fish communities of Orinoco floodplain lakes. Natl. Geogr. Res. 6:319–328.

Rodriguez-Gironés, M. A., and L. Santamaría. 2006. A new algorithm to calculate the nestedness temperature of presence–absence matrices. J. Biogeogr. 33:924–935.

Sachs, J. D., J. E. M Baillie, W. J. Sutherland, P. R. Armsworth, N. Ash, J. Beddington, T. M. Blackburn, B. Collen, B. Gardiner, K. J. Gaston, et al. 2009. Biodiversity conservation and the millenium development goals. Science 325(5947):1502–1503.

Soininen, J. 2008. The ecological characteristics of idiosyncratic and nested diatoms. Protist 159:65–72.

Soule, N. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39–47.

Taylor, C. M., and M. L. Warren. 2001. Dynamics of species composition of stream fish assemblages: environmental variability and nested subsets. Ecology 82:2320–2330.

Tockner, K., F. Schiemer, C. Baumgartner, G. Kum, E. Weigand, L. Zweimuller, and J. V. Ward. 1999. The Danube restoration project: species diversity patterns across connectivity gradients in the floodplain system. Regul. Rivers Res. Manage. 15:245–258.

Ulrich, W., M. Almeida-Neto, and N. J. Gotelli. 2009. A consumer's guide to nestedness análisis. Oikos 118:3–17.

Ulrich, W. and N. J. Gotelli. 2007. Null model analysis of species nestedness patterns. Ecology 88:1824–1831.

Watts, B. D. 1996. Landscape configuration and diversity hotspots in wintering sparrows. Oecologia 108:512–517.

Winemiller, K. O., S. Tarim, D. Shormann, and J. B. Cotner. 2000. Fish assemblage structure in relation to environmental variation among Brazos river oxbow lakes. Trans. Am. Fisheries Soc. 129:451–468.

Wright, D. H., B. D. Patterson, G. M. Mikkelson, A. Cutler, and W. Atmar. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia 113:1–20.

Wright, D. H. and J. H. Reeves. 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92:416–428.