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Article

Biodiversity and conservation of conservation priority fish species in the Nicaraguan volcanic crater lakes

Jeffrey K. McCrary

Biodiversity Research Group, Universidad Nacional Autónoma de Nicaragua, Managua 11001, Nicaragua; jmccrary2@yahoo.com

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Abstract: The theory of island biogeography was tested in Nicaraguan volcanic crater lakes, colonized by fish from the older and larger source Nicaraguan Great Lakes. Spearman correlations of ranked molecular phylogenetic diversity in the Midas cichlid species complex (*Amphilophus* cf. *citrinellus*) were significant ($p \leq 0.05$) or marginally significant ($0.05 < p \leq 0.10$) with diversity with crater lake age in three of four data sets tested. Correlations were noted with deepwater area, the product of littoral area and age, and with the product of horizontal and vertical barriers between the crater lakes and the nearest source lakes divided by the product of littoral area and age. By treating the Midas cichlid species complex as a single taxon, ranked fish taxon richness in each lake correlated significantly with lake age, littoral area, and with the product of age and littoral area. These results support the concept that littoral area and lake age may be factors in the colonization of volcanic crater lakes from the source lakes, and the amount of deep water in a lake as well as lake age may be important factors in speciation in the Midas cichlid species complex. Seven species from the crater lakes have been classified as Critically Endangered by the IUCN.

Keywords: island biogeography; genetic diversity; endemic species

1. Introduction

The neotropics face socio-political dilemmas regarding natural resource use policies which fragment and degrade habitats for species in peril [1]. Countries such as Nicaragua, within the Mesoamerica biodiversity hotspot [2], face biodiversity conservation issues from the distinct disadvantage of poverty [3] and recurring political conflict [4].

On a worldwide scale, islands contribute to biodiversity disproportionately to the area they contain. Several considerations regarding the biodiversity of islands now constitute aspects of a foundational theoretical foundation of ecology [5,6]. Islands may be inhabited by relatively low numbers of species because of factors such as distance from nearby land masses from which dispersal may occur, and size and suitability of island habitats which may limit the number of species that are sustained.

Furthermore, evolutionary processes on islands may vary substantially from those on large land masses. A repeated motif of island biogeography is the appearance of endemic species which evolved in the isolated ecosystems following colonization. The classic example of Darwin's finches [7] is now included in a generalized theory of adaptive radiation [8].

Island endemics are particularly susceptible to environmental change [9]. Human-mediated processes on local and global scales place numerous island endemic species at risk [10].

The concept of island biogeography has been extended to what are called habitat islands which can apply to both naturally fragmented systems and to anthropogenic isolations [11]. Freshwater lake biodiversity has been interpreted using island biogeographic theory, in which the roles of land and water as habitat and barrier are reversed from the traditional approach [12,13].

Several quaternary volcanoes on the western side of Nicaragua containing standing water within their craters, can be treated as ecological and evolutionary "islands", with no lake exceeding 21 km^2 surface area [14]. These lakes lack any open water connection to any other aquatic habitat. The "continental" aquatic counterpart to these lakes, the much older and larger Nicaraguan Great Lakes, comprise 9000 km^2 total surface area, and contain several dozen fish species, in comparison to the relatively depauperate fish fauna of all surveyed volcanic crater lakes [15].

These volcanic crater lakes are now considered to be among the most important habitats for biodiversity in Mesoamerica. Numerous endemic fish species, many of these are classified as conservation priority species, thanks to their small and very poorly characterized populations, miniscule ranges, and numerous, poorly characterized environmental challenges, are known to inhabit some of these lakes. The fish fauna of eight of the Nicaraguan crater lakes were compared in terms of dimensions of physical barriers to dispersal from the Nicaraguan Great Lakes, crater lake ages and dimensions, and water chemical and physical factors; expected trends were statistically significant in lake age and lake size [14].

Midas cichlid morphologies in the crater lakes correlated differently than overall fish diversity, however. Morphological divergence in the Midas cichlid species group from its source populations in the Nicaraguan Great Lakes correlated negatively with littoral zone area, whereas elongation in the Midas cichlid species group and overall variation in body shape both correlated significantly with lake mean depth [16].

The application of the island theory of biogeography to the fish fauna of the Nicaraguan volcanic crater lakes was revisited, with considerations regarding new information about the fish biodiversity and lake parameters. The environmental challenges, conservation aspects, and research needs in each lake are discussed.

2. Study sites and methods

The locations of the volcanic crater lakes in western Nicaragua, are shown in **Figure 1**. The fish fauna and the geographical characteristics of eight of these lakes, with reference to the theory of island biogeography, was previously surveyed [14,17,18] and some lake age estimates have been revised [19]. Although the taxonomic descriptions in the Midas cichlid species complex have been conducted only partially and unevenly across the crater lakes, genetic breadth of the species group has been estimated in several lakes [20,21].

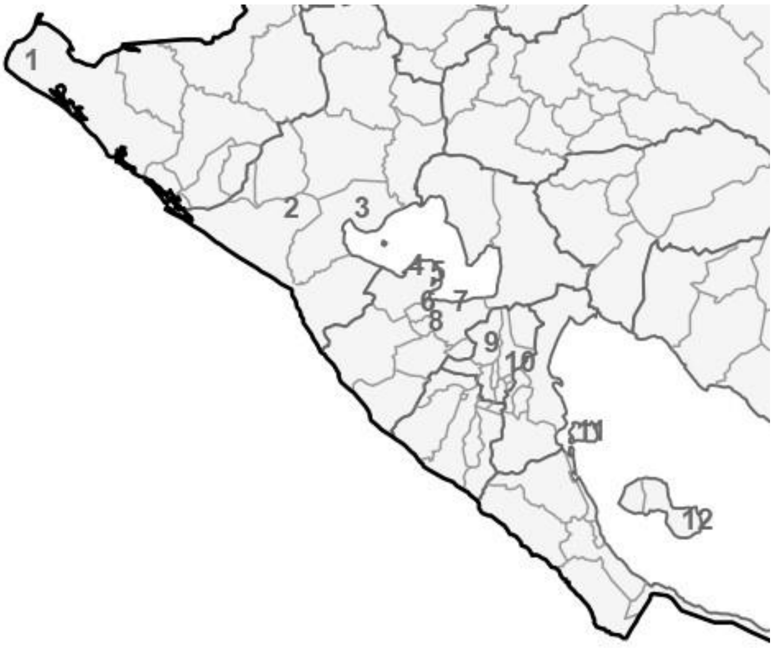

Figure 1. Map of western Nicaragua with locations of volcanic crater lakes.
Note: 1-Lake Cosigüina; 2-Lake Asososca León; 3-Lake Monte Galán; 4-Lake Apoyeque; 5-Lake Xiloá; 6-Lake Asososca Managua; 7-Lake Tiscapa; 8-Lake Nejapa; 9-Lake Masaya; 10-Lake Apoyo; 11-Lake Zapatera; 12-Lake Maderas.

The ranked species diversity of volcanic crater lakes was compared with ranked physical/chemical/geological parameters: Surface area, littoral area (less than 30 m depth), deepwater area (more than 30 m depth), maximum depth, mean depth, volume, pH, conductivity, dissolved solids, turbidity, horizontal and vertical isolation, and estimated lake age. Because the taxonomy of the Midas cichlid species group is the product of fine-scale speciation that has been unevenly researched across the volcanic crater lakes, it was treated a single taxon in an analysis of the eight volcanic crater lakes where surveys have been conducted.

The island biogeographic influences on diversity within the Midas cichlid species group was treated by correlating ranked lake parameters with ranked breadth of molecular variances. Geiger and coauthors [20] reported mitochondrial control region haplotype numbers in each other above-mentioned volcanic lakes, minus Lake Monte Galán and Lake Asososca Managua. Barluenga and Meyer [21] reported mitochondrial haplotype richness, mitochondrial haplotype diversity, and microsatellite gene diversity in each lake except Lake Monte Galán and Lake Tiscapa. Ranked genetic breadth for each of these four parameters was correlated by ranked parameters as above.

Confidence intervals of 95% were considered significant ($p \leq 0.05$), of 90% considered marginally significant ($0.05 < p \leq 0.10$), on Spearman correlations of ranked parameters [22] with the ranked taxon or molecular phylogenetic diversity.

All protected or noted conservation priority fish species found in the volcanic crater lakes are discussed.

3. Results

The statistical significance of each correlation between ranked lake physical/chemical/geological parameters and ranked fish diversity parameters is shown in **Table 1**.

Table 1. Spearman correlation coefficients (r) and confidence levels (p) for ranked fish diversity correlation with ranked volcanic crater lake parameters.

Parameter	**Correlation 1**		**Correlation 2**		**Correlation 3**		**Correlation 4**		**Correlation 5**	
	R	**P**	**R**	**P**	**R**	**P**	**R**	**P**	**R**	**P**
Area	0.540	0.17	0.714	0.11	–0.086	0.87	0.200	0.70	0.772	**0.07**
Littoral Area	0.700	**0.05**	0.029	0.96	–0.543	0.27	0.429	0.40	0.714	0.11
Maximum depth	–0.024	0.95	0.429	0.33	–0.257	0.62	–0.657	0.16	0.086	0.87
Mean depth	0.270	0.52	0.657	0.16	–0.143	0.79	–0.086	0.87	0.314	0.54
Volume	0.466	0.24	0.714	0.11	–0.143	0.79	–0.486	0.33	0.543	0.27
pH	–0.519	0.19	–0.657	0.16	0.257	0.62	–0.371	0.47	–0.771	**0.07**
Conductivity	0.172	0.68	–0.086	0.87	–0.543	0.27	–0.028	0.96	0.143	0.79
Dissolved solids	–0.062	0.88	–0.143	0.79	–0.543	0.27	–0.028	0.96	0.143	0.79
Turbidity	0.596	0.12	0.829	**0.04**	0.348	0.50	0.058	0.91	0.145	0.78
Age	0.700	**0.05**	0.886	**0.02**	–0.029	0.96	0.771	**0.07**	0.772	**0.07**
Horizontal distance	0.209	0.62	–0.143	0.79	–0.371	0.47	0.086	0.87	–0.257	0.62
Vertical barrier	0.258	0.54	0.466	0.35	0.257	0.62	0.600	0.21	0.143	0.79
HxV	0.135	0.75	0.200	0.70	0.143	0.79	0.429	0.40	–0.314	0.54
HxV/Age	0.454	0.26	0.600	0.21	0.257	0.62	0.543	0.27	0.143	0.79
HxV/(AgexLit)	0.670	**0.07**	0.771	**0.07**	0.314	0.54	0.829	**0.04**	0.314	0.54
AgexLit	–0.850	**0.01**	0.657	0.16	–0.143	0.79	0.771	**0.07**	0.771	**0.07**
Deepwater Area	0.370	0.37	0.754	**0.08**	–0.200	0.70	0.029	0.96	0.829	**0.04**

Notes: Significant ($p \leq 0.05$) and marginally significant ($0.5 \leq p \leq 0.10$) values are in bold text.
Correlation 1-Taxon diversity in eight volcanic crater lakes: Apoyeque, Apoyo, Asososca León, Asososca Managua, Masaya, Monte Galán, Tiscapa, Xiloá. All Midas cichlid taxa are counted as a single taxon.
Correlation 2-Mitochondrial control region haplotype richness [20] in the Midas cichlid species complex in six lakes (Apoyeque, Apoyo, Asososca León, Masaya, Tiscapa, Xiloá).
Correlation 3-Mitochondrial haplotype richness [21] in the Midas cichlid species complex in six lakes (Apoyeque, Apoyo, Asososca León, Asososca Managua, Masaya, Xiloá).
Correlation 4-Mitochondrial haplotype diversity [21] in the Midas cichlid species complex in six lakes (Apoyeque, Apoyo, Asososca León, Asososca Managua, Masaya, Xiloá).
Correlation 5-Microsatellite gene diversity [21] in the Midas cichlid species complex in six lakes (Apoyeque, Apoyo, Asososca León, Asososca Managua, Masaya, Xiloá).
Lake parameter codes: HxV-product of horizontal distance and vertical barrier; HxV/Age-product of horizontal distance and vertical barrier, divided by lake age; HxV/(AgexLit)-product of horizontal distance and vertical barrier, divided by product of lake age and littoral area.

The following parameter rankings correlated with the rankings of taxon richness across eight lakes, when considering the Midas cichlid species complex as a single taxon: lake age ($p = 0.05$); littoral area ($p = 0.05$); rankings of the product lake age and littoral area correlated significantly with taxon richness ($p = 0.01$). The product horizontal and vertical isolation divided by the product of lake age and littoral area correlated marginally with taxon richness ($p = 0.07$).

To analyze the correlation between diversity within the Midas cichlid species complex and the above-mentioned parameter rankings across volcanic crater lakes, the rankings of results of molecular diversity analyses which were conducted across several lakes were used. Lake age correlated significantly with ranked mitochondrial control region haplotype numbers [20] (p = 0.02), as did turbidity (p = 0.04), and a marginal correlation was seen with the product horizontal and vertical barrier dimensions divided by the product lake age and surface area (p = 0.07) and with the ranked deepwater area (p = 0.08) across six of these lakes (no data were presented for lakes Monte Galán and Asososca Managua).

Barluenga and Meyer [21] presented three different parameters of Midas cichlid species complex molecular diversity, in six lakes (no results were presented for Lakes Tiscapa and Monte Galán). Ranked mitochondrial haplotype richness did not correlate with any ranked lake parameter. Ranked mitochondrial haplotype diversity, however, correlated significantly with the ranked product vertical and horizontal isolation divided by the product lake age and littoral area (p = 0.04), and marginally with ranked age (p = 0.07), and with the ranked product lake age by littoral area (p = 0.07). Ranked microsatellite gene diversity ranked marginally with pH (p = 0.07) and with lake age (p = 0.07), and with the product littoral area and lake age (p = 0.07), and significantly (p = 0.04) with ranked deepwater area.

Conservation priority species present in the Nicaraguan volcanic crater lakes are presented in **Table 2**. Two species are protected by Nicaraguan law which prohibits their capture between 20 May and 20 July [23]. Although those two species are not given conservation priority status on the IUCN Red List [24], seven species are designated as Critically Endangered, six as Vulnerable, and two are listed as Near Threatened, totaling seventeen species receiving some level of conservation priority status nationally or internationally.

Table 2. Threatened and protected fish taxa in each volcanic crater lake.

Family	**Species**	**Status**	**Apoyeque**	**Apoyo**	**Asososca Managua**	**Asososca León**	**Masaya**	**Monte Galán**	**Tiscapa**	**Xiloá**
Dorosomatidae	*Dorosoma chavesi*	NT					X	X		X
Cichlidae	*Amphilophus amarillo*	VU								X
Cichlidae	*Amphilophus astorquii*	CR		X						
Cichlidae	*Amphilophus chancho*	CR		X						
Cichlidae	*Amphilophus flaveolus*	CR		X						
Cichlidae	*Amphilophus globosus*	CR		X						
Cichlidae	*Amphilophus sagittae*	VU								X
Cichlidae	*Amphilophus supercilius*	CR		X						
Cichlidae	*Amphilophus tolteca*	VU			X					
Cichlidae	*Amphilophus viridis*	VU								X

Table 2. (*Continued*).

Family	Species	Status	Apoyeque	Apoyo	Asososca Managua	Asososca León	Masaya	Monte Galán	Tiscapa	Xiloá
Cichlidae	*Amphilophus xiloaensis*	VU								X
Cichlidae	*Amphilophus zaliosus*	CR		X						
Cichlidae	*Hypsophrys nematopus*	NT					X			X
Cichlidae	*Parachromis dovii*	LC*					X			X
Cichlidae	*Parachromis managuensis*	LC*	X	X	X	X	X	X	X	X
Atherinopsidae	*Atherinella jiloaensis*	CR								X
Atherinopsidae	*Atherinella sardina*	VU		X	X		X	X		

Note: Conservation status designations from IUCN Red List [24] and Nicaraguan law [23]: LC-Least Concern; NT-Near Threatened; VU-Vulnerable; CR-Critically Endangered; *-protected from capture 20 May–20 July.

The twelve volcanic crater lakes are protected by regulations that apply to volcanic crater lakes [25] as well as legislation which applies to official protected areas with governmental administration [26–28] (**Table 3**).

Table 3. Protected area designations which incorporate volcanic crater lakes in Nicaragua.

Volcanic Crater Lake	Protected Area	Location	Number of known fish species	Red List Species	Known invasive species
Lake Apoyeque	Chiltepe Peninsula Nature Reserve	12°14′48″ N 86°20′32″ W	4	0	0
Lake Apoyo	Lake Apoyo Nature Reserve	11°55′26″ N 86°00′42″ W	9	7	2
Lake Asososca León	Cerro Negro, Las Pilas, El Hoy, and Asososca Volcanic Complex Nature Reserve	12°26′06″ N 86°39′50″ W	3	0	1
Lake Asososca Managua	Lake Asososca Managua Nature Reserve	12°08′14″ N 86°18′55″ W	4	2	0
Lake Cosigüina	Volcano Cosigüina Nature Reserve	12°58′59″ N 87°33′52″ W	-	-	-
Lake Maderas	Volcano Maderas National Park	11°26′39″ N 85°30′37″ W	-	-	-
Lake Masaya	Volcano Masaya National Park	11°57′33″ N 86°07′33″ W	11	3	0
Lake Monte Galán	Momotombo Volcanic Complex Nature Reserve	12°26′21″ N 86°34′31″ W	9	2	0
Lake Nejapa	Lake Nejapa Nature Reserve	12°07′12″ N 86°19′13″ W	0	0	1
Lake Tiscapa	Lake Tiscapa Nature Reserve	12°08′22″ N 86°16′14″ W	3	0	0
Lake Xiloá	Chiltepe Peninsula Nature Reserve	12°13′16″ N 86°19′18″ W	19	7	0
Lake Zapatera	Zapatera Archipielago National Park	11°46′06″ N 85°51′27″ W	-	-	-

4. Discussion

4.1. Species diversity correlations with biogeographical parameters

The volcanic crater lakes present some of the expected patterns of island biogeography in this analysis. The parameter which most consistently correlated with lake biodiversity was lake age, which produced significant or marginally significant correlations in four of the five tests. The product of age and littoral area, and the product of horizontal and vertical barriers from the respective Nicaraguan Great Lakes divided by the product of age and littoral area, correlated significantly or marginally significantly with three of the tested biodiversity parameters (**Table 1**).

The fish diversity native to eight volcanic crater lakes in Nicaragua is the product of two distinct sets of processes. In the first, species are established in volcanic crater lakes after dispersal into the lakes, presumably from the nearer of the two Nicaraguan Great Lakes. It is arguable that Lake Xiloá, which was likely formed by subsidence of Lake Managua after the formation of the volcanic crater within it, has undergone a process of extirpations of species whose populations are no longer viable in the relatively limited area and habitat remaining after Lake Xiloá became an isolated body of water, sometime within the past few thousand years.

In the remaining seven lakes in which native fish biodiversity was compared, dispersal of fishes into the lakes to establish reproducing populations required processes such as hurricanes, birds, or even humans. Genetic drift has been little surveyed among these species in the lakes, with only the description of *Atherinella jiloaensis* in Lake Xiloá suggesting that even a relatively small physical barrier for dispersal, in this context, may be sufficient for a fish population to undergo allopatric speciation after colonization, in what may be far less than ten thousand generations. In the absence of information that could further clarify the mechanism of formation of this species in Lake Xiloá, it is best considered to be the product of allopatric speciation after isolation of the crater lake population from the older population inhabiting the Nicaraguan Great Lakes. Whether other speciation events have occurred in the isolated populations of these crater lakes, aside from the Midas cichlid species complex, is not known [15].

In contrast to other species found in the Nicaraguan volcanic crater lakes, the Midas cichlid species complex has undergone a dramatic, complex set of speciations, presumably during the same evolutionary period that other species inhabit the volcanic crater lakes, but without any evidence of such processes in those species. Eleven species have been described to date from these "islands", with unique species flocks expected in each volcanic crater lake, based upon by between-lake molecular phylogenetic comparisons [20,21], a within-lake molecular phylogenetic analysis in Lake Apoyo [29], and mate selection by direct observation [30,31].

Doubtless, any attempt to assess the validity of island biogeographical theory in explaining the taxon diversity of the Nicaraguan volcanic crater lakes is confounded by the unevenly examined taxonomic status of the Midas cichlid species complex in these lakes. Waid and coauthors [14] found ranked taxa richness correlated significantly with taxa richness and three ranked factors: littoral lake area, total lake area, and lake age; and marginally significantly with ranked lake volume. The present analysis produced similar results. Ranked taxon richness correlated with ranked lake age, and with ranked littoral area. Ranked taxon richness correlated marginally with the ranked product of the two, and significantly with the ranked product of the vertical barrier between the volcanic crater lakes with the horizontal distance from the nearest source lake, divided by the product of age and littoral area. Ranked taxon richness correlated less well, just beyond the chosen criterion for marginal significance, with ranked total lake area in the present study (p = 0.17; **Table 1**).

The ranked molecular phylogenetic diversity in the Midas cichlid species complex, as found in the four data sets analyzed herein, showed similar patterns of correlations as that above. Three of the four ranked data sets correlated significantly or marginally with lake age. Two correlated significantly or marginally with the product of lake age and littoral area, and two with the product of horizontal distance from the source lakes and vertical barrier, divided by the product of lake age and littoral area, coinciding with the correlations found in the other taxa (**Table 1**). The coincidence of correlations across these data sets suggests that some of the lake parameters influence fish biodiversity in the Nicaraguan volcanic crater lakes across all the taxa found there.

Notably, lake depth, found to be a factor in Midas cichlid phylogenetic diversity in another study [16], which did not produce a significant correlation here. Nonetheless, the total lake area minus the littoral area, which equates to the area of a lake found at greater than 30 meters depth [14], produced one significant correlation and one marginally significant correlation (**Table 1**), supporting the hypothesis by Kautt and coauthors [16] that deep water may factor in the radiation of colonizing Midas cichlids in the volcanic crater lakes.

The relatively limited role of distance and height barriers to colonization found herein and in other studies [14,16] lend credibility to the suggested hypothesis of anthropogenic colonizations in some of the volcanic crater lakes. Although intentional species introductions in the Nicaraguan volcanic crater lakes have set alarms in recent history [14,32] (**Table 3**) humans moving biodiversity is not new. Cultural factors could weigh more heavily over the past 10,000 or so years that humans inhabited the Pacific region of Nicaragua than the physical barriers considered here.

All Midas cichlid species described to date from the Nicaraguan volcanic crater lakes have been given conservation priority designations on the IUCN Red List (**Table 2**). The remaining Midas cichlid species complex forms are classified as either *Amphilophus citrinellus*, which corresponds to the thin-lipped forms typically known as Midas cichlids, or *Amphilophus labiatus*, which corresponds to the thick-lipped forms known commonly as the red devil cichlid, which have poorly determined genetic relationships, and are treated for the purposes of this discussion as wastebasket taxa. The IUCN Red List has classified *A. citrinellus* as Least Concern, and *A. labiatus* has not been classified [24].

Interestingly, the jaguar cichlid, *P. managuensis*, does not appear to undergo speciation in unique habitats as does the Midas cichlid. Aside from the immensely important questions of evolutionary biology, however, lies a vital implication of the speciation occurring within the Midas cichlid species complex, which is that each volcanic crater lake contains species that inhabit small, restricted habitats, and thus require particular attention to the security of their populations and habitats.

There is considerable taxonomic confusion regarding the forms of the livebearer genus *Poecilia* found in the Mesoamerica region [33]. Most of the volcanic crater lakes contain at least one reported taxon of the genus [14].

4.2. Legal framework for protection of volcanic crater lakes

There are several laws and regulations that directly apply to the protection of biodiversity and their habitat in Nicaragua. Most, but not all, the lakes are incorporated into protected areas in the National System of Protected Areas. The General Environmental Law 217 establishes this system, in which all protected areas are administered according to management plans commissioned by the Ministry of the Environment and Natural Resources (MARENA), approved by the National Assembly, and subsequently published in the official state media [27]. **Table 3** shows the protected areas which include volcanic crater lakes within their borders.

The General Environmental Law 217 and the regulations developed from this law [26,27] provide for a system of protected species is maintained and updated yearly. All activities within protected areas are regulated by MARENA and management plans specific to each protected area are in place [28].

Nicaragua protects species through a prohibition on capture, in which some species are prohibited entirely from capture and a season on takes is permitted on other species. Two fish species documented in the Nicaraguan crater lakes are protected by an official fishing seasonal ban [23]. The fifteen IUCN Red-Listed fish species, however, do not automatically receive recognition or protection in Nicaragua [24].

All volcanic crater lakes in Nicaragua are afforded another level of protection, through the Nicaraguan Obligatory Technical Normative 05002-08. Through this instrument, controls are set on fishing, erosion, construction, and wastewater in the vicinity of volcanic crater lakes, as well as use of motorized water vehicles, use of contaminating substances, introduction of non-native species, and commercial activities. This regulation applies to activities in the lakes and within the volcanic crater or, where the crater limit is not well-defined, up to 1500 meters from the lake in a Protection Zone [25].

4.3. Land-use effects on the volcanic crater lakes

Sedimentation is a general phenomenon of the crater lakes, which have no outlet for suspended solid materials. As mentioned above, some volcanic crater lakes are facing grave situations, whereas with others, the situation is latent. Increased demands on land use may be driving deforestation, land-use change, and forest fires which all accelerate the sedimentation process when occurring within the volcanic crater interior. Any fish biodiversity native to Lake Nejapa was possibly lost due to sediments entering the lake. The lake level was as little as one meter depth over much of the lake by 1972, due to sedimentation and reduction in water level from increased transpiration caused by deforestation in the area [34]. Almost complete desiccation occurred during an ENSO event in the early 1990’s [35] (p. 233).

Lake Apoyo is affected by deforestation for fuelwood for local consumption and development of properties for vacation homes and tourism. Lake levels were measured over more than two decades, during which more than two meters were lost. Many rocky reef substrates, important for nesting for some fish species in the lake, are potentially lost as the lake level recedes and as erosion from development of the crater interior accelerates the runoff of sediments into the lake. During this period, ion concentrations also increased significantly [36].

Access to the volcanic crater containing Lake Asososca Managua is tightly controlled, as this lake continues to be used as a municipal water source, and the surrounding lands in the crater interior are owned by the government of Nicaragua [35] (p. 248). The crater holding the lake is surrounded by an urban environment. At approximately one kilometer north of the crater holding this lake lies a chemical industrial complex, including an oil refinery and abandoned chemical production facilities with contaminated soils in their vicinity, which must be considered in water extraction management to prevent subterranean water flow reversal [37].

Lake Tiscapa receives large quantities of sediments and urban solid waste from urban stormwater drainage diverted into the lake. The quantities have affected its bathymetric profile and cause periodic fish kills [38].

Lake Masaya is contaminated by large quantities of solid waste from municipalities along the eastern and southern edge of its crater, and poorly treated municipal wastewater on entering from the eastern edge of the crater [35] (p. 301), resulting in periodic fish kills [17].

4.4. Invasive species

Introductions of non-native species are prohibited in protected areas [26,27] and in the volcanic crater lakes regardless of whether they are within protected area boundaries [25]. Nonetheless, fish species introductions have occurred within some of the volcanic crater lakes, as is discussed below.

Although current legislation prohibits the introduction of non-native species into volcanic crater lakes, several introductions have already occurred, some with devastating consequences. Tilapia (*Oreochromis* spp.), a cichlid fish group commonly used in aquaculture, have been introduced into different Nicaraguan volcanic crater lakes. In Lake Asososca León, *Oreochromis mossambicus* was introduced, most likely during the 1960’s, and a small population continues has been documented in the lake [32]. The impacts of this introduction are unknown, largely because very little research on the fishes of this lake have been conducted.

Lake Apoyo has undergone three different introductions of non-native species. During the 1980’s a small cage-aquaculture experiment using *Oreochromis aureus* was conducted in the northern littoral region of the lake. Fishes escaped from this procedure were seen in the lake as much as a decade later. During the 1990’s another cage aquaculture activity was conducted using its congener, *Oreochromis niloticus*. Large numbers of escapees were detected in the lake, and submerged vegetation, once abundant, was eliminated, apparently consumed by the ranging tilapias [32].

In 1991, a small number of individuals of a species found in nearby watersheds, the lurking predator eleotrid fish *Gobiomorus dormitor*, was introduced into Lake

Apoyo. The population of this species rose exponentially during the ensuing six-year period. The introduced population was found to be consuming the threatened atherinopsid *Atherinella sardina* native to the lake, and, also, conducting cannibalism on younger individuals of its own species [39].

A sampling of Lake Nejapa in 2004 by the author produced only the introduced species *O. niloticus*. There are no records of how the species was introduced.

4.5. Looking forward

The Nicaraguan volcanic crater lakes are habitats for many endemic fish species of high conservation priority, disproportionate to the attention given to their life histories and environmental concerns. Seven species native to the volcanic crater lakes of Nicaragua are Red-Listed as Critically Endangered; six (*Amphilophus astorquii*, *Amphilophus chancho*, *Amphilophus flaveolus*, *Amphilophus globosus*, *Amphilophus supercilius*, *Amphilophus zaliosus*) are described species of the Midas cichlid species complex endemic to Lake Apoyo, and one (*A. jiloaensis*) is an atherinopsid species endemic to Lake Xiloá [24] (**Table 2**). These species demand considerably more attention by scientists and conservation professionals. A limited amount of life-history information specific to the six Midas cichlid species from Lake Apoyo is currently known [30,31], and no life-history information specific to the seventh Critically Endangered species exists.

Six species are listed as Vulnerable in the IUCN Red List [24] (**Table 2**). Four (*Amphilophus amarillo*, *Amphilophus viridis*, *Amphilophus sagittae*, *Amphilophus xiloaensis*) are members of the Midas cichlid species complex endemic to Lake Xiloa. One (*Amphilophus tolteca*) is endemic to Lake Asososca Managua, and the sixth (*A. sardina*) inhabits inhabits Lake Apoyo, Lake Asososca Managua, Lake Masaya, and Lake Monte Galán, along with the San Juan River watershed including the Nicaraguan Great Lakes [15]. Research has been conducted on the ecology of the Midas cichlid group in Lake Xiloá, although these studies have conflated the two species *A. xiloaensis* with the later discovered *A. viridis* [18]. Little is known of the ecology or life history of *A. sardina* [39–42].

Two species have Near Threatened status: the cichlid *Hypsophrys nematopus*, found in Lake Masaya and Lake Xiloá, and the dorosomatid *Dorosoma chavesi*, found in those two lakes plus Lake Monte Galán. Some aspects of the reproductive biology of the former have been published [43], but nothing is known about the ecology or life history of the latter [17].

In synthesis, too little information is known about the life histories, ecologies, and environmental status of almost all the fifteen Red Listed species found in the volcanic crater lakes of Nicaragua. Beyond these species are the species of the Midas cichlid species complex that have yet to be discovered. All these species demand reviews of the status of their populations.

All the remaining lakes with populations of the Midas cichlid species complex (Apoyeque, Asososca León, Tiscapa, Monte Galán) need additional study to determine if endemic species can be identified among their populations.

All the volcanic crater lakes are managed within the National System of Protected Areas, which uses management plans to strategize conservation strategies in each protected area. As management plans for the volcanic crater lakes are updated, there should be directed attention to the ichthyological biodiversity these lakes contain. Particular attention should be placed on the internationally recognized IUCN Red-List conservation assessments of the species found in these lakes.

The fish diversity native to some volcanic crater lakes have never been evaluated. The likelihood of unique, even endemic, taxa in these lakes, merits consideration. It is recommended to perform integrated field surveys of the aquatic fauna, limnology, and water conditions in Lakes Zapatera, Cosigüina, Maderas, and Nejapa, and to set strategies toward the protection of the biodiversity found in each in the respective management plans.

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