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On the brink – investigating biodiversity in endangered crater lakes of the Amber Mountains National Park (Madagascar)

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ABSTRACT

1. Madagascar's biodiversity is vanishing at an alarming pace. The documentation of this loss has so far focused on terrestrial habitats and organisms. Eight volcanic crater lakes in the Amber Mountains National Park (Northern Madagascar) and surroundings were investigated for the first time to describe limnological conditions and aquatic biodiversity. Seven of the lakes were affected by deforestation/logging and fish introduction and only one lake was assumed to have remained in pristine condition. In the deeper lakes (> 5 m) steep physico-chemical gradients and anoxic hypolimnia were observed.

2. Algae, hydrozoans, nematodes, rotifers, annelids, copepods, cladocerans, ostracods, and mites were identified to genus or species level. The majority were taxa with a cosmopolitan or tropicopolitan distribution. The highest number of afrotropical and endemic species were recorded within the crustaceans.

3. Multivariate analysis of species communities revealed significant differences between lakes in deforested and forested catchments. Introduced alien fish had no detectable effect on species assemblages.

4. Illegal harvest of timber was observed within the National Park and drug plantations are less than 1 km away from the last pristine crater lake. If deforestation continues at the current rate, which is likely under the prevailing political situation, the last undisturbed lake communities may be altered in the near future.

5. There is an urgent need for taxonomic research to assess the biodiversity of algae and micrometazoa. Highest priority should be given to pristine freshwater ecosystems within protected areas.

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KEY WORDS: algae; alien species; biogeography; deforestation; invertebrates; island; lake; taxonomy

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INTRODUCTION

The island of Madagascar is among the top hotspots for biodiversity conservation worldwide (Myers *et al.*, 2000; Ganzhorn *et al.*, 2008; Vieites *et al.*, 2009). More than 90% of all plants, 100% of native amphibian and mammal species, 92% of reptiles and 44% of birds occur nowhere else. This high level of endemism predominantly results from radiation of African founder individuals arriving during the Cenozoic (65.5 Ma to present) and from relict species radiating after the island separated from the African mainland (183–158 Ma), Antarctica (130 Ma), and India (96–65 Ma; Vences *et al.*, 2009).

Besides an extraordinary diversity in terrestrial organisms, Madagascar has also been recognized as a global hotspot of freshwater biodiversity (Groombridge and Jenkins, 1998). In the last two decades of the 20th century the number of newly described species of aquatic insects and fish had increased exponentially (Benstead et al., 2003). However, owing to incomplete species inventories and taxonomic difficulties, the degree of endemism in small planktonic and benthic organisms is difficult to assess. There is evidence for endemism especially for copepods (Dussart, 1982), but also for some freshwater algae (e.g. desmids (West and West, 1895; Bourrelly and Couté, 1991; Coesel, 2002) and benthic diatoms (Metzeltin and Lange -Bertalot, 2002)).

Taxonomic research on Malagasy freshwater algae and micrometazoa is still scarce. There are no systematic species inventories available and current knowledge is based on random samples mostly covering specific groups of organisms from different habitats. First surveys of the Malagasy freshwater algal flora were provided by West and West (1895), Fritsch (1914), Manguin (1941), Bourrelly and Leboime (1946) and Bourrelly and Manguin (1949). More detailed algological investigations are available for diatoms (Spaulding and Kociolek, 1998a, b; Metzeltin and Lange -Bertalot, 2002), desmids (Bourrelly and Couté, 1991; Coesel, 2002) and chrysophytes (Hansen, 1996). Taxonomic research on micrometazoa was conducted predominantly until the 1960s (DeGuerne and Richard, 1893; Brehm, 1930, 1948; Kiefer, 1930). Most studies were based on samples taken by the director of the Institut des recherches scientifiques de Madagascar, Renauld Paulian, who sent the material to various taxonomists (Rotifera: Berzins, 1960, 1973, 1982;

Harpacticoida: Chappuis, 1952, 1954, 1956; Calanoida: Brehm, 1951, 1952a, b, c, 1953, 1954; Cyclopoida: Lindberg, 1951a, b, 1952, 1953; Kiefer 1952, 1954, 1955; Cladocera: Brehm, 1953). Brehm (1960) gave an account of freshwater Crustacea collected during the Austrian Madagascar expedition in 1958. After this period of intensive taxonomic work on freshwater micrometazoa few publications appeared (Dussart, 1982; Segers, 1992; Fiers, 2002).

Madagascar's biological richness is threatened by massive habitat destruction. Forty per cent of rainforest cover was lost between 1950 and 2000 (Harper et al., 2007; Wikipedia, 2012). Deforestation currently continues at a rate of about 0.5% per year (57 000 ha; Mongabay, 2011). Although the country possesses 46 legally protected areas covering almost 1.7 million hectares (2.89% of total territory), habitat destruction still proceeds at an alarming pace. A peak in illegal logging was observed during the political turmoil in 2009. Schuurman and Lowry (2009) spoke of a 'Madagascar rosewood massacre', because 625 containers of hardwood worth approximately US \$ 130 million illegally left the country in 2009. Most of the trees were felled in protected mountain reserves in Northern Madagascar (Marojeji, Masoala, and Amber Mountains). During sampling in May 2009 the illegal harvest of rosewood and palisander (Dalbergia spp.) was witnessed on several occasions.

Deforestation not only changes terrestrial habitats but causes increased sediment delivery and nutrient input into rivers and lakes and hence alters physico-chemical conditions, species composition and trophic interactions in aquatic habitats as well (Benstead *et al.*, 2003). Loss of forest cover has already caused a shift from persistent to intermittent flow in the streams draining the northern and eastern slopes of the Amber Mountains and the Tsaratanana Massif (Raxworthy *et al.*, 2008).

Following habitat destruction, invasive species are regarded as the second leading cause of species extinction and endangerment worldwide (Sala *et al.*, 2000). A number of alien fish species have been stocked in pristine Malagasy fresh waters causing severe changes to entire ecosystems and being detrimental to various groups of animals (Canonico *et al.*, 2005). For instance, there is a strong correlation between the introduction of exotic fish and the decline of native fish in Madagascar (Reinthal and Stiassny, 1991; Sparks and Stiassny, 2003), but no information is available about their impact on plankton and benthos communities in Malagasy lake ecosystems.

Finally, the warming trends reported for Madagascar equal or exceed global averages (Raxworthy *et al.*, 2008). A drier climate will accelerate the destruction of montane rainforests in the Amber Mountains National Park. At its lower level the thinning of the protective canopy exposes the forest to sunlight and drying wind thereby increasing the risk of wildfires.

Benstead *et al.* (2003) defined three major objectives to conserve the remaining Malagasy freshwater biodiversity: (1) Survey efforts have to be directed at remote regions that have no inventories for freshwater biota. (2) Systematic and ecological studies of poorly known taxonomic groups must be undertaken. (3) Top conservation priority should be given to intact freshwater ecosystems that are situated within protected areas.

Today, only a few pristine volcanic crater lakes on the entire island remain surrounded by primary rainforest (Schabetsberger et al., 2009a). The two largest clusters of crater lakes are within or near the borders of the volcanic massifs of the Amber Mountains and the Tsaratanana (Bemanevika area) National Parks in Northern Madagascar. The Bemanevika lakes were found to be the last refuge for only a few individuals of the Madagascar pochard, a duck proclaimed extinct and rediscovered in 2006 (TWSG News, 2006), but the catchment already exhibits fragmented pockets of rainforest near the lakes. A single isolated crater lake in the Makira protected area, Lake Amparihibe, also appeared to be pristine (Schabetsberger et al., 2009a). It was reached by a 1-day boat journey and a 3-day march through rainforest. Nevertheless, the illegal harvest of hardwood trees was witnessed more than half way along the trail. These last examples of undisturbed lentic species communities, which have persisted before and since the arrival of man on Madagascar approximately 2300 years ago (Burney et al., 2004), should therefore be given high priority in future conservation measures.

The aim of this study was a preliminary limnological characterization of lakes in the Amber Mountains National Park and its surroundings. Preliminary species lists of planktonic and benthic organisms are presented and the impact of deforestation and stocking with alien fish species on freshwater communities is analysed. The samples were collected during a single expedition mounted during times of political unrest and increasing illegal timber harvest within the Amber Mountains National Park (Schuurman and Lowry, 2009; personal observations). Although we were unable to collect replicate samples and measure nutrient chemistry, these first baseline data are provided to support future conservation efforts.

STUDY AREA

The Amber Mountains are a large stratovulcano in northern Madagascar (c. 2500 km^2). Radiometric ages of lavas range from $12.1 \pm 0.2 \text{ Ma} ({}^{40}\text{Ar} - {}^{39}\text{Ar})$ in the north west to $0.83 \pm 0.02 \text{ Ma} ({}^{40}\text{K} / {}^{40}\text{Ar})$ in the central part, suggesting that the volcanism was active from at least the middle Miocene. The massif is formed by 'hundreds of lava flows, plugs, spatter cones, tuff rings, pyroclastic flows, and pyroclastic fall deposits' (Cucciniello *et al.*, 2011 and references therein). Several lakes fill tuff rings that represent the youngest volcanic activity of the complex.

In 1958 the French Colonial Forces established the first Malagasy National Park in the Amber Mountains massif. Today the Park protects 18 200 ha of mid-altitude montane rainforest lying at altitudes ranging from 850–1475 m. Five volcanic crater lakes are situated within (here numbered (1-3); (7)), or at the edge of the forest (8), while three lakes at lower altitude (4-6) are outside the park and are surrounded by savannah (Figures 1, 2; Table 1). Lake Manonja (7) remains the only unstocked lake surrounded by primary rainforest, whereas the savannah has already reached the southern shore of Lake Fantany (8). Also, 'khat' (Catha edulis - a drug common in East Africa) plantations are closing in on Lake Manonja and are now less than 1 km away.

During French occupation, a forest station operated at the park entrance near Joffreville (A. Randimbison, personal communication). From there black bass (*Micropterus salmoides*) and carp (*Cyprinus carpio*) were introduced into three out of five lakes in the centre of the park (Mahasarika (1), Malio (2), Taranta (3)). In addition, tilapia (*Tilapia rendalli*) and mosquitofish (*Gambusia affinis*) are found today in the lake closest to the park entrance (Mahasarika (1)). The lakes surrounded by savannah (Mahery (4), Antagnavo (6), and Antagnavo ely (5)) contain tilapias together with endemic cichlids and are inhabited by crocodiles (*Crocodylus niloticus*).

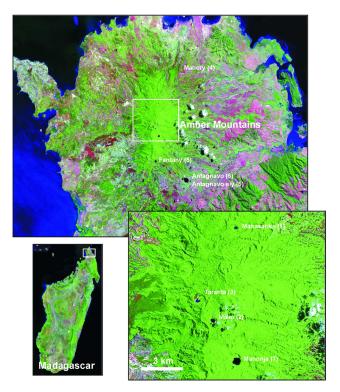


Figure 1. Location of the sampling sites in the Amber Mountains National Park and surroundings (green: forested (lakes 1, 2, 3, 7, 8); red: savannah (4, 5, 6)).

METHODS

Field work lasted from 16 to 23 May 2009 during the beginning of the dry season. The savannah lakes were sampled only from the shoreline or the outflow (Lake Antagnavo), because of the danger of crocodiles. In the other lakes the maximum depth was measured from an inflatable dinghy with a portable gauge. Depth-specific water samples were collected at the deepest point with a Schindler-Patalas trap and profiles of temperature (thermometer within trap), pH, conductivity (Hanna Combo electrode), and oxygen (Hach HQ 40d) were measured. Integrated qualitative plankton samples were taken with a 30 µm plankton net by retrieving the net from near bottom layers or throwing out the net from the shore. In addition, samples were collected in different littoral habitats (sediment, macrophytes). All samples were filtered through a $30\,\mu\text{m}$ net and preserved in 4%formaldehyde. Quantitative phytoplankton samples were collected from the water surface at the deepest point in lakes Mahasarika, Malio and Taranta (200 mL unfiltered lake water) and at three different depths in lakes Manonja (1, 5, 9 m depth) and Fantany (1, 7, 15m) and preserved with Lugol's solution.

In the laboratory Lugol-preserved phytoplankton samples were analysed following recommendations for counting and biovolume calculations using the Utermöhl technique (Rott, 1981). Species were determined from Lugol and formaldehyde-preserved plankton samples (algae in general: E. Rott; Zygnematophyceae: R. Lenzenweger and E. Rott). Zooplankton and zoobenthos samples were stained with Rose Bengal, sorted under a stereo microscope and determined to genus or species (hydrozoans: R.D. Campbell; nematodes: W. Traunspurger; rotifers: R. Schabetsberger; annelids: S. Gaviria; cladocerans: A. Kotov; copepods: F. Fiers; ostracods: C. Meisch; mites: S. Mahunka).

Species assemblages were analysed with non-linear multidimensional scaling (NMDS; Kruskal, 1964) using presence/absence data of all taxa occurring in more than one lake (103 out of 276 taxa, mean 21.5 ± 15.3 SD) and the Kulczynski index (Faith et al., 1987; Legendre and Legendre, 1998) as a measure of dissimilarity. Using the same index, an agglomerative hierarchical clustering of the data was computed (Kaufman and Rousseeuw, 1990). Ordination diagrams and fitted environmental vectors, as well as clustering solutions, indicated a strong pattern related conductivity. to Subsequently an Analysis of Variance Using Distance Matrices (Anderson, 2001; McArdle and Anderson, 2001) was applied to test the null hypothesis of no relationship between species assemblages and conductivity. All computations were coded in R (R Development Core Team, 2011) using base packages plus the vegan library (Oksanen et al., 2011).

RESULTS

Description of lakes

Data on physical conditions and algae are presented in Figures 3 and 4.

Mahasarika (1, Figure 2(a))

The 4.8 m deep crater lake is oversaturated with oxygen down to 4 m depth. A strong gradient in pH and high total algal biomass result from a bloom of *Monoraphidium contortum*, *Microcystis wesenbergii*, *Cylindrocystis* sp., and *Cosmarium* sp. It is said that the lake feeds the water supply for the town of Antsiranana (Diego-Suarez; A. Amba, personal communication), although to

Malio



A PARTY OF THE PARTY OF





Antagnavo ely

Manonja



Antagnavo



Fantany



Figure 2. Photographs of the lakes in the Amber Mountains National Park and surroundings.

our knowledge there are no hydrological studies available to confirm this.

Malio (2, Figure 2(b))

The highest lake within the National Park was saturated with oxygen throughout the 4 m deep water column. Weak gradients in all parameters indicated frequent mixing of the shallow lake. Phytoplankton biomass was dominated by Cyanobacteria (*Cyanodictyon* sp., *Microcystis pulverea*, *Microcystis* sp.) and Dinophyceae (*Peridinium volzii*).

Taranta (3, Figure 2(c))

The lake is only 0.9 m deep and well oxygenated. Phytoplankton was dominated by Zygenematophyceae (*Cosmarium pygmaeum*), Chlorophyceae (*Coelastrum sphaericum*) and Dinophyceae (*Peridiniopsis elpatiewskyi*).

Mahery (4, Figure 2(d))

Several small islands indicate a shallow depth of the lake (probably < 3 m). The near-shore water is characterized by comparatively higher conductivity

Lake Number	Malagasy Name	Foreign Name	Sampling Date	Altitude (m)	Max.Length (m)	Max.Length Max. Depth (m) (m)	Temp. (°C)	Cond. (µS cm ⁻¹)	Hq	$\begin{array}{c} Oxygen \\ (mg \ L^{-1}) \end{array}$	Oxygen (% sat)	Fĭsh
_	Mahasarika	Petit Lac	16.05.2009	1060	280	4.8	24.6	28	9.28	8.24	115	Tilapia rendalli, Cyprinus carpio, Micropterus salmoides, Gamhusia affinis
7	Malio	Grand Lac	16.05.2009	1335	360	4.0	20.6	31	8.41	7.97	105	Cyprimus carpio, Micropterus salmoides
3.	Taranta	Maudit	18.05.2009	1250	720	0.9	19.8	56	8.22	8.09	103	Cyprinus carpio, Micropterus salmoides
4 v	Mahery Antagnavo	Mahery Sacré small	19.05.2009 20.05.2009	364 348	765 190	Shallow 2.5	26.1 25.9	218 202	6.87 7.16	1 1		Tilapia rendalli, Paratilapia sp.* Tilapia rendalli, Paratilapia sp.*, Burdedani, cometari
9	ery Antagnavo	Sacré	20.05.2009	367	1660	ė	26.1	231	8.74			Ttycnocnromus sp. Tilapia rendalli, Paratilapia sp.*, Phydrodyromic sp.*
7 8	Manonja Fantany	Texier Fantany	22.05.2009 23.05.2009	1034 810	630 780	25 32	22.7 25.4	61 75	9.01 9.06	8.72 8.01	113 108	a tythoduced fish, eels* no introduced fish, eels*?

and slightly acidic conditions within a dense belt of the non-native water hyacinth Eichhornia crassipes.

Antagnavo ely (5, Figure 2(e))

The small crater lake in the south east of Lake Antagnavo is also surrounded by floating carpets of E. crassipes. Similar to Lake Mahery, surface conductivity was > 200 μ S cm⁻¹ and pH was just above neutral.

Antagnavo (6, Figure 2(f))

The water in the outflow was characterized by high pH and conductivity (Table 1). Crocodiles are fed regularly in ritual ceremonies.

Manonja (7, Figure 2(g))

Lake Manonja is the most pristine freshwater ecosystem in the Amber Mountains National Park. The protected crater lake is 25 m deep and exhibited steep physico-chemical gradients. Beyond 15m depth the water was anoxic. A phytoplankton bloom resulted in high pH values in shallow water. The algal community was dominated by Cyanobacteria (Anabaena sp., Cyanodictyon sp.). So far the lake has not been stocked with alien fish and is said to contain large numbers of native eels (Anguilla sp.; A. Amba, personal communication). Plantations of 'khat' (Catha edulis) are only an hour's walk away from the lake and numerous felled rosewood trees were seen in the area.

Fantany (8, Figure 2(h))

The deepest lake in the Amber Mountains National Park (32m) is situated at the border between rainforest and savannah. Similar to Lake Manonja, steep physico-chemical gradients were found and the water was anoxic beyond 15 m depth. Phytoplankton was dominated by Cyanobacteria (Microcvstis pulverea; M. wesenbergii, Cvanothece Bacillariophyceae (Synedra sp.). sp.) and Dinophyceae (Peridiniopsis elpatiewskyi). According to information from local people crocodiles have been introduced into the lake, but so far no fish have been stocked. The illegal harvest of hardwood was witnessed near the lake.

Species assemblages

In total, 142 algal, 1 hydrozoan, 23 nematode, 56 rotifer, 12 annelid, 15 copepod, 16 cladoceran, 8 ostracod, and 3 mite taxa were recorded

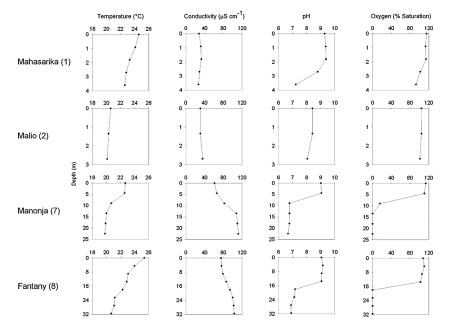


Figure 3. Depth profiles of temperature, conductivity, pH, and oxygen in four lakes of the Amber Mountains National Park.

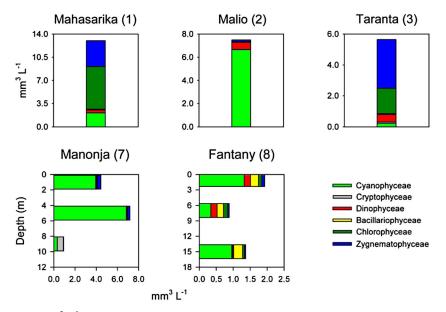


Figure 4. Phytoplankton biomass (mm³ L⁻¹) at 0.5 m depth in shallow lakes (top panels) and at three different depths in the deeper lakes (> 5 m, bottom panels) within the Amber Mountains National Park.

(Appendix). The highest species richness was observed in the belt of water hyacinth of Lake Mahery (4) (Figure 5). Crustacean species exhibited a lower proportion of cosmopolitan or widely distributed taxa than the other groups of organisms. Truly endemic morpho-species (3) were predominantly found within the copepods and they were restricted to lakes within the park boundaries (Appendix).

Ordinations and clustering solutions clearly corroborate differences in species assemblages with regard to conductivity and surrounding vegetation (Figure 6). Conductivity was significantly related to vegetation (one-way ANOVA, $F_{1,6}$: 152, *P*: <0.0001) with mean 50.2 μ S cm⁻¹ ± 20.2 SD for forest and 217 μ S cm⁻¹ ± 14.5 for savannah environments. Analysis of Variance Using Distance Matrices confirmed that conductivity is non-randomly related to species patterns and explains roughly one-third of the variability in the species matrix (R-squared: 0.34, $F_{1,6}$: 3.05, *P*: 0.003, *P*-values obtained by 999 permutations). The same holds true for surrounding vegetation (2-level factor: forest and savannah) when used as

predictor variable (R-squared: 0.33, $F_{1,6}$: 2.98, *P*: 0.016, 999 permutations). The effect of introduced fish on species assemblages and richness was also tested. Analysis of Variance was applied using

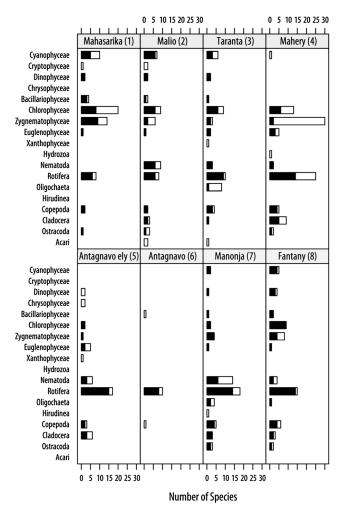


Figure 5. Total number of species grouped at higher taxonomic level (Appendix). The stack bars give the number of species occurring in more than one lake (solid black) and the fraction of species encountered only within the named lake (white).

Distance Matrices and one-way ANOVA of log-transformed species richness. Only spurious relationships were found.

Ordination of lake communities (Figure 6(a)) shows a distinct pattern with regard to conductivity. Likewise, items display a clear group structure when ordination scores are labelled according to the surrounding environment. Independent cluster analyses (Figure 6(b)) corroborate the validity of the ordination configuration. In addition, clustering analyses suggest a hierarchical structure in the data, embedding the three savannah lakes in a group with two forest lakes of intermediate (7) and low conductivity (2).

DISCUSSION

Species communities differed between lakes situated in forested compared with deforested catchments. In turn forest cover was strongly correlated with water conductivity, being four times higher in lowland lakes surrounded by savannah. Increased sediment input through soil erosion probably leads to changes in algal and micrometazoan communities (Lott et al., 1994; Alin et al., 2002), single sampling cannot although provide conclusive evidence. Deforestation proceeded from the lowlands around Lake Antagnavo (6) towards the foothills of the Amber Mountains within the last millennium (Burney et al., 2004) and has now reached Lake Fantany (8). We hypothesize that sediment cores would reveal clear changes in species communities after the arrival of humans, that are not paralleled in the forest lakes. In this respect the lakes would be promising targets for palaeolimnological research.

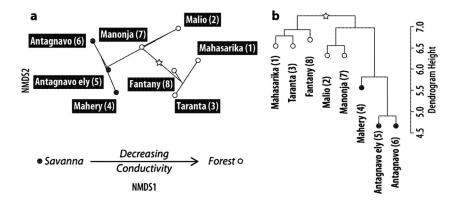


Figure 6. Ordination diagram and cluster dendrogram based on the Kulczynski index computed with presence/absence data. a: NMDS Ordination (stress: 7.85) with sample sites connected by a cluster dendrogram. The star denotes the root of the dendrogram (see b.). The fit of conductivity onto the ordination is shown as a symbolic arrow (R-squared: 0.91, P: 0.002, p-values based on 999 permutations). b: Agglomerative Nesting Clustering (agglomerative coefficient: 0.15) with tips coded according to the surrounding vegetation.

Owing to their sheltered position and nutrient-rich volcanic bedrock, all deeper crater lakes within the park exhibited strong physico-chemical gradients, anoxic hypolimnia and phytoplankton blooms. The highest epilimnetic algal biomass was recorded in the lake with four introduced alien fish species. This might have resulted from the absence of larger crustacean grazers because of size-selective fish predation. Unfortunately quantitative phytoplankton samples from lowland lakes were lost.

No significant differences were detected between species assemblages of the stocked and the two unstocked lakes. The effects of fish were probably masked by more prominent factors such as forest cover. In the highest lake of the National Park introduced fish coexisted with the only endemic calanoid copepod species **Tropodiaptomus** madagascariensis. This is different from the results obtained from a high-altitude lake of similar size and depth, where native calanoids were eliminated within a decade after stocking (Schabetsberger et al., 2009b; see also Knapp et al., 2001). Either the lake was stocked fairly recently by carrying fish from the lower lakes uphill, or the copepod can tolerate size-selective fish predation. However, we still postulate that palaeolimnological work would reveal changes within the species communities after fish introduction, especially as the introduced cyprinids, tilapias, and mosquitofish prey on different trophic levels from detritus to algae to insect larvae (Zambrano et al., 1999; Fishbase, 2012).

Deforestation and introduction of alien species does not necessarily result in a decrease in species richness. For example, the large belt of Eichhornia in Lake Mahery (4) probably decreases the pH to slightly acidic conditions through CO_2 accumulation (Rai and Munshi, 1979), enabling the development of a rich desmid flora surpassing any other sampling site in its diversity. However, the high proportion of taxa that were recorded only once suggests that the single preliminary survey does not warrant a comparison of overall species richness between lakes, especially as the largest crater lake could only be sampled in the outflow.

Similar to other isolated crater lakes on Madagascar, islands of Oceania and in West Africa (Schabetsberger *et al.*, 2004, 2009a, c), a large proportion of species were cosmopolitans or widely distributed taxa. Only within the crustaceans did tropicopolitan and afrotropical faunal elements predominate. The Mozambique Channel may not be a barrier for the transport of their propagules with wind, rain and water birds. Truly endemic species were predominantly found within the copepods, which seem to have limited dispersal abilities (Schabetsberger *et al.*, 2009c).

On the other hand there is growing evidence that many freshwater algal and micrometazoan morpho-species are actually complexes of cryptic species with more restricted distributions (Gómez et al., 2002; Fawley et al., 2004; Belyaeva and Taylor, 2009). In addition, some species that could only be determined to genus level may be new endemic taxa. Hence, remote lakes on islands may still harbour comparatively higher proportions of genetically isolated lineages of microorganisms (Schröder and Walsh, 2007). With several species of higher plants and animals on the brink of extinction in Madagascar, conserving potentially undescribed planktonic and benthic organisms has low priority. At present the lakes attract international conservation efforts only if 'flagship' bird species occur (e.g. the Madagascar pochard, Avthva innotata (TWSG News, 2006)). With the current state of knowledge it is impossible to understand distribution patterns and the full degree of endemicity in Malagasy freshwater organisms.

Conserving the lakes and their catchments from further deterioration is difficult. The Amber Mountains and their lakes are protected as an internationally recognized National Park, which is the highest status of protection in Madagascar. However, the raiding of the forests is highly organized and well funded, as 1 m³ of rosewood yields US\$ 3000 (Wikipedia, 2012). Encampments of loggers may invite the introduction of alien fish into the last unstocked lake. The eradication of alien fish populations by intensive gill netting and seining (Knapp and Matthews, 1998) might help temporarily to restore more natural conditions in the shallow, already stocked lakes and could be achieved with comparatively little funding. However, as long as some precious timber can leave the country, the remaining forests will be steadily depleted and the impact on lake ecosystems will increase.

The protection of National Parks from illegal timber harvest is difficult and requires frequent controls of armed rangers, which is unrealistic under the current political situation. Owing to international pressure timber exports were banned in 2010 (Bohannon, 2010), but on 18 January 2012 Madagascar's Minister of the Environment has re-authorized the export of 'all categories of natural forest-sourced primary products' (Mongabay, 2012). Only international loans financing conservation efforts in Madagascar coupled with political pressure may ease the current situation, although it is likely only to slow down the depletion until the trees finally become too scarce to be harvested economically. Subsequently, slash-and-burn agriculture, tree cutting, honey extraction, and bushmeat hunting will commence within the degraded catchments. By then, the Amber Mountains lake communities will resemble those from lowland areas.

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REFERENCES

- Alin RS, O'Reilly M, Cohen AS, Dettman DL, Palacios-Fest MR, McKee BA. 2002. Effects of land use change on aquatic biodiversity: a view from the paleorecord of Lake Tanganyika, East Africa. *Geology* 30: 1143–1146.
- Anderson M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Belyaeva M, Taylor DJ. 2009. Cryptic species within the *Chydorus sphaericus* species complex (Crustacea:Cladocera) revealed by molecular markers and sexual stage morphology. *Molecular Phylogenetics and Evolution* **50**: 534–546.
- Benstead JP, DeRham PH, Gattolliat J-L, Gibon F-M, Loiselle PV, Sartori M, Sparks JS, Stiassny MLJ. 2003. Conserving Madagascar's freshwater biodiversity. *BioScience* 53: 1101–1111.
- Berzins B. 1960. Neue Rotatorienarten aus Madagaskar. Mémoires de la Institut Scientifique de Madagascar 14: 1–6.
- Berzins B. 1973. Zwei neue *Euchlanis* –Arten, Rotatoria. *Zoologischer Anzeiger* **190**: 125–127.
- Berzins B. 1982. Zur Kenntnis der Rotatorienfauna Madagaskars. AV centralen i. Lund: Lund, Sweden.
- Bohannon J. 2010. Madagascar's forests get a reprieve but for how long? *Science* **328**: 23–25.
- Bourrelly P, Leboime R. 1946. Notes sur quelques algues d'eau douce de Madagascar. *Biologisch Jaarbock, Dodonea* 13: 75–111.
- Bourrelly P, Manguin E. 1949. Contribution à l'étude de la flore algale d'eau douce de Madagascar. Le lac de Tzimbazaza. Mémoires de la Institut Scientifique de Madagascar 2: 161–190.
- Bourrelly P, Couté A. 1991. Desmidiées de Madagascar. Bibliotheca Phycologica 86. Gebrüder Borntraeger: Berlin-Stuttgart.
- Brehm V. 1930. Notizen zur Cladocerenfauna Madagaskars. *Archiv für Hydrobiologie* **21**: 679–686.
- Brehm V. 1948. Nuevos copepodos de Madagascar. Publicaciones Instituto de Biologia applicada Barcelona 5: 77–84.
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- Brehm V. 1951. Pseudodiaptomus pauliani. Der erste Vertreter der Pseudodiaptomiden in der madegassichen Fauna. Mémoires de la Institut Scientifique de Madagascar 6: 419–425.
- Brehm V. 1952a. Cladoceren und calanoide Copepoden von Madagaskar. Mémoires de la Institut Scientifique de Madagascar 7: 37–46.
- Brehm V. 1952b. Anadiaptomus madagascariensis Rylov (Copepoda Diaptomidae). Le Naturaliste Malgache 3: 159–162.
- Brehm V. 1952c. Anadiaptomus poseidon nov. gen., nov. spec. aus Madagaskar. Anzeiger der österreichischen Akademie der Wissenschaften 89: 23–27.
- Brehm V. 1953. Cladocères et copépodes calanoides de Madagascar. *Le Naturaliste Malgache* **5**: 151–152.
- Brehm V. 1954. Pseudodiaptomus batillipes, spec. nov., ein zweiter Pseudodiaptomus aus Madagaskar. Sitzungsberichte der österreichischen Akademie der Wissenschaften, Mathematisch – Naturwissenschaftliche Klasse 1: 603–607.
- Brehm V. 1960. Ergebnisse der österreichischen Madagaskar-Expedition 1958: 1. Beitrag zur Kenntnis der Crustacea madegassischer Stillgewässer. *Mémoires de la Institut Scientifique de Madagascar* 14: 39–58.
- Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodmann SM, Wright HT, Jull AJT. 2004. A chronology for late prehistoric Madagascar. *Journal of Human Evolution* 47: 25–63.
- Canonico GC, Arthington A, McCrary JK, Thieme ML. 2005. The effects of introduced tilapias on native biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* **15**: 463–483.
- Chappuis PA. 1952. Copépodes harpacticoides psammiques de Madagascar. Mémoires de la Institut Scientifique de Madagascar 7: 145–160.
- Chappuis PA. 1954. Recherches sur la faune interstitielle des sediment marins et d'eau douce a Madagascar. IV. Copépodes harpacticoides psammiques de Madagascar. Mémoires de la Institut Scientifique de Madagascar 9: 45–73.
- Chappuis PA. 1956. Presence a Madagascar du genre *Echinocamptus: E. pauliani* n.sp. *Mémoires de la Institut Scientifique de Madagascar* **10**: 35–42.
- Coesel PFM. 2002. Taxonomic and biogeographical notes on Malagasy desmids (Chlorophyta, Desmidiaceae). Nordic Journal of Botany 22: 239–256.
- Cucciniello C, Melluso L, Morra V, Storey M, Rocco I, Franciosi L, Grifa C, Petrone CM, Vincent M. 2011. New ⁴⁰Ar-³⁹Ar ages and petrogenesis of the Massif d'Ambre volcano, northern Madagascar. *Geological Society of America Special Papers* **478**: 257–281.
- DeGuerne J, Richard J. 1893. *Canthocamptus grandidieri*, *Alona cambouei*, nouveaux entomostraces d'eau douce de Madagascar. *Mémoires de la Societé zoologique de France* **96**: 234–244.
- Dussart BH. 1982. Crustacés Copèpodes des eaux intérieures. Faune de Madagascar. 58. ORSTOM, CNRS: Paris.
- Faith FP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**: 57–68.
- Fawley MW, Fawley KP, Buchheim MA. 2004. Molecular diversity among communities of freshwater microchlorophytes. *Microbial Ecology* 48: 489–499.
- Fiers F. 2002. The genus *Haplocyclops* Kiefer, 1952 (Copepoda, Cyclopoida, Cyclopidae): redescription of the type-species, *H. gudrunae*, and its congeners. *Hydrobiologia* **474**: 155–169.
- Fishbase. 2012. http://www.fishbase.org. (30 March 2012)
- Fritsch FE. 1914. Contribution to our knowledge of the freshwater algae of Africa. I. Some freshwater algae from Madagascar. *Annales de Biologie Lacustre* 7: 40–59.

Aquatic Conserv: Mar. Freshw. Ecosyst. (2012)

- Ganzhorn JU, Lowry PP, Schatz GE, Sommer S. 2008. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. *Oryx* **35**: 346–348.
- Gómez A, Serra M, Carvalho GR, Lunt DH. 2002. Speciation in ancient cryptic species complexes: evidence from the molecular phylogeny of *Brachionus plicatilis* (Rotifera). *Evolution* **56**: 1431–1444.
- Groombridge B, Jenkins M. 1998. Freshwater Biodiversity. A Preliminary Global Asessment. World Conservation Monitoring Centre (WCMC), Biodiversity Series no. 8, World Conservation Press. WCMC: Cambridge.
- Hansen P. 1996. Silica-scaled Chrysophyceae and Synurophyceae from Madagascar. Archiv für Protistenkunde 147: 145–172.
- Harper GJ, Steininger MC, Tucker CJ, Juhn D, Hawkins F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34: 325–333.
- Kaufman L, Rousseeuw PJ. 1990. Finding Groups in Data: an Introduction to Cluster Analysis. Wiley: New York.
- Kiefer F. 1930. Zur Kenntnis freilebender Copepoden Madagaskars. *Zoologischer Anzeiger* **87**: 42–46.
- Kiefer F. 1952. Haplocyclops gudrunae n.gen. et n.sp., ein neuer Ruderfußkrebs (Crustacea Copepoda) aus Madagaskar. Zoologischer Anzeiger 149: 240–243.
- Kiefer F. 1954. Neue Cyclopoida Gnathostoma (Crustacea Copepoda) aus Madagaskar. I. Cyclopininae and Halicyclopinae. Zoologischer Anzeiger 153: 308–313.
- Kiefer F. 1955. Neue Cyclopoida Gnathostoma (Crustacea Copepoda) aus Madagaskar. II. Cyclopinae. Zoologischer Anzeiger 154: 222–232.
- Knapp RA, Matthews KR. 1998. Eradication of nonnative fish by gill-netting from a small mountain lake in California. *Restoration Ecology* 6: 207–213.
- Knapp RA, Matthews KR, Sarnelle O. 2001. Resistence and resilience of Alpine lake fauna to fish introductions. *Ecological Monographs* **71**: 401–421.
- Kruskal JB. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115–129.
- Legendre P, Legendre L. 1998. Numerical Ecology, 2nd edn, Elsevier: Amsterdam.
- Lindberg K. 1951a. Cyclopides de Madagascar I. Mémoires de la Institut Scientifique de Madagascar 5: 187–195.
- Lindberg K. 1951b. Cyclopides de Madagascar II. Mémoires de la Institut Scientifique de Madagascar 6: 427–437.
- Lindberg K. 1952. Cyclopides de Madagascar III. Mémoires de la Institut Scientifique de Madagascar 7: 53–67.
- Lindberg K. 1953. Cyclopides de Madagascar IV. Mémoires de la Institut Scientifique de Madagascar 8: 11–17.
- Lott A-M, Siver PA, Mariscano LJ, Kodoma KP, Moeller RE. 1994. The paleolimnology of a small waterbody in the Pocono Mountains of Pennsylvania, USA: reconstructing 19th–20th century specific conductivity trends in relation to changing land use. *Journal of Paleolimnology* **12**: 75–86.
- Manguin E. 1941. Contribution à la connaisance des Diatomées d'eau douce de Madagascar. *Revue Algologique* **12**: 153–157.
- McArdle B, Anderson M. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82: 290–297.
- Metzeltin D, Lange–Bertalot H. 2002. Diatoms from the "Island Continent" Madagascar. *Iconographia Diatomologica*, 11. Koeltz Scientific Books: Königstein.
- Mongabay. 2011. http://rainforests.mongabay.com/20madagascar. htm (2 November 2011)
- Mongabay. 2012. http://news.mongabay.com/2012/0229rosewood_ban_lifted.html (30 March 2012)
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.

- Oksanen J, Guillaume Blanchet F, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2011. Vegan: Community Ecology Package. R version 2.0-0. http://vegan.r-forge. r-project.org/
- Rai DN, Munshi JD. 1979. The influence of thick floating vegetation (Water hyacinth: *Eichhornia crassipes*) on the physico-chemical environment of a freshwater wetland. *Hydrobiologia* **62**: 65–69.
- Raxworthy, CJ, Pearson RG, Rabibisoa N, Rakotodrazafy AM, Ramanamanjato J-P, Raselimanana AP, Wu S, Nussbaum RA, Stone DA. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology* 14: 1703–1720.
- R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria.
- Reinthal PN, Stiassny MLJ. 1991. The freshwater fishes of Madagascar: a study of an endangered fauna with recommendations for a conservation strategy. *Conservation Biology* **5**: 231–243.
- Rott E. 1981. Some results from phytoplankton counting intercalibrations. *Schweizerische Zeitschrift für Hydrologie* **43**: 34–63.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A *et al.* 2000. Biodiversity global biodiversity scenarios for the year 2100. *Science* **287**: 1770–1774.
- Schabetsberger R, Drozdowski G, Drozdowski I, Jersabek CD, Rott E. 2004. Limnological aspects of two tropical crater lakes (Lago Biao and Lago Loreto) on the island of Bioko (Equatorial Guinea). *Hydrobiologia* 524: 79–90.
- Schabetsberger R, Rott E, Friedl G, Drozdowski G, Razafinadranaivo E, Holmes C. 2009a. First limnological characterization of the tropical crater lake Amparihibe in the Makira Protected Area, Madagascar. *Eco-Mont* 1: 43–52.
- Schabetsberger R, Luger M, Drozdowski G, Jagsch A. 2009b. Only the small survive – monitoring long-term changes in the zooplankton community of an Alpine lake after fish introduction. *Biological Invasions* **11**: 1335–1345.
- Schabetsberger R, Drozdowski G, Rott E, Lenzenweger R, Jersabek CD, Fiers F, Traunspurger W, Reiff N, Stoch F, Kotov AA *et al.* 2009c. Losing the bounty? Investigating species richness in isolated freshwater ecosystems of Oceania. *Pacific Science* 63: 153–181.
- Schröder T, Walsh EJ. 2007. Cryptic speciation in the cosmopolitan *Epiphanes senta* complex (Monogononta, Rotifera) with the description of new species. *Hydrobiologia* **593**: 129–140.
- Segers H. 1992. Taxonomy and zoogeography of the rotifer fauna of Madagascar and the Comoros. *Journal of African Zoology* **106**: 351–361.
- Schuurman D, Lowry PP. 2009. The Madagascar rosewood massacre. *Madagascar Conservation and Development* 4: 98–102.
- Sparks JS, Stiassny MLJ. 2003. Introduction to the freshwater fishes. In *The Natural History of Madagascar*, Goodman SM, Benstead JP (eds). University of Chicago Press: Chicago; 849–863.
- Spaulding SA, Kociolek JP. 1998a. New *Gomphonema* (Bacillariophyceae) species from Madagascar. *Proceedings* of the California Academy of Sciences **50**: 361–379.
- Spaulding SA, Kociolek JP. 1998b. The diatom genus *Orthoseira*: ultrastructure and morphological variation in two species from Madagascar with comments on nomenclature in the genus. *Diatom Research* **13**: 133–147.

- TWSG News. 2006. Madagascar Pochard rediscovered. *The Bulletin of the Threatened Waterfowl Specialist Group* **15**: 8.
- Vences M, Wollenberg KC, Vietes DR, Lees DC. 2009. Madagascar as a model region of species diversification. *Trends in Ecology & Evolution* 24: 456–465.
- Vieites DR, Wollenberg KC, Andreone F, Koehler J, Glaw F, Vences M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences USA* 106: 8267–8272.
- West W, West GS. 1895. A contribution to our knowledge of the freshwater algae of Madagascar. *Transactions of the Linnean Society London, Botany* **5**: 41–90, plates 5–9.
- Wikipedia. 2012. http://en.wikipedia.org/wiki/Illegal_logging_ in_Madagascar. (2 July 2012)
- Zambrano L, Perrow MR, Macías-García C, Hidalgo V. 1999. Impact of introduced carp (*Cyprinus carpio*) in subtropical shallow ponds in Central Mexico. *Journal of Aquatic Ecosystems Stress and Recovery* **6**: 281–288.

APPENDIX

Freshwater algae, Hydrozoa, Nematoda, Rotifera, Annelida, Copepoda, Cladocera, Ostracoda, and Acari found in the eight lakes of the Amber Mountains National Park (1–8, Table 1) and surroundings and their known distribution (afrotrop. = afrotropical; austral. = Australian; circumtrop. = circumtropical; cosm. = cosmopolitan; holarct. = holarctic; nearct. = nearctic; neotrop. = neotropical; orient. = oriental; palaearct. = palaearctic; tropicopol. = tropicopolitan). Circumtropical: distribution predominantly between the Tropics of Cancer ($23^{\circ}27'$ N) and Capricorn ($23^{\circ}27'$ S); Tropicopolitan: distribution throughout the tropical and subtropical zone (up to app. 34° N and S), but at higher latitudes, if local temperature regimes permit

Group	Species Names	Lake Number	Biogeography
Cyanophyceae	Anabaena sp.	1,2,7,	
Cyanophyceae	Aphanocapsa delicatissima W. West & G.S. West, 1912	1,3,	cosm.
Cyanophyceae	Chroococcus limneticus Lemmermann, 1898	3,	cosm.
Cyanophyceae	Chroococcus sp.	1,	
Cyanophyceae	Cyanodictyon sp.	2,7,	
Cyanophyceae	Cyanothece sp.	2,8,	
Cyanophyceae	Cylindrospermopsis africana Komárek & Kling, 1991	1,	afrotrop.?
Cyanophyceae	Geitlerinema splendidum (Greville) Anagnostidis, 1989	4,	cosm.
Cyanophyceae	Merismopedia tenuissima Lemmermann, 1898	1,	cosm.
Cyanophyceae	Microcystis aeruginosa (Kützing) Kützing, 1846	1,2,8	cosm.
Cyanophyceae	Microcystis comperei Komárek, 1984	1,	
Cyanophyceae	Microcystis protocystis Crow, 1932	8,	circumtrop.
Cyanophyceae	Microcystis pulverea (Wood) Forti, 1907	2,8,	cosm.
Cyanophyceae	Microcystis wesenbergii (Komárek) Komárek, 1968	1,3,8,	cosm.
Cyanophyceae	Microcystis sp.	1,	
Cyanophyceae	Oscillatoria sp.	3,	
Cyanophyceae	Planktolyngbya limnetica (Lemmermann)	1,2,3,8,	cosm.
- J. I. J.	J. Komárková-Legnerová & G. Cronberg, 1992))-)-)	
Cyanophyceae	Planktolyngbya undulata Komárek & Kling, 1991	3,	afrotrop.
Cyanophyceae	Radiocystis sp.	2,	······································
Cryptophyceae	Chroomonas acuta Utermöhl, 1925	2,	cosm.
Cryptophyceae	Cryptomonas tetrapyrenoidosa Skuja, 1948	2,	cosm.?
Cryptophyceae	Cryptomonas sp.	1,	
Dinophyceae	Gymnodinium sp.	5,	
Dinophyceae	Peridiniopsis elpatiewskyi (Ostenfeld) Bourrelly, 1968	1,3,8,	cosm.?
Dinophyceae	Peridinium cf. pusillum (Pénard) Lemmermann, 1901	8,	cosm.?
Dinophyceae	Peridinium volzii var. cinctiforme M.Lefèvre, 1932	2,7,	endemic?
Dinophyceae	Peridinium sp. 1	2,3,8,	
Dinophyceae	Peridinium sp. 2	1,8,	
Dinophyceae	Wolozynskia sp.	5,	
Chrysophyceae	Mallomonas sp.	5,	
Chrysophyceae	Spiniferomonas sp.	5,	
Bacillariophyceae	Aulacoseira ambigua (Grunow) Simonsen, 1979	1,2,8,	cosm.
Bacillariophyceae	Aulacoseira granulata (Ehrenberg) Simonsen, 1979	1,3,7,	cosm.
Bacillariophyceae	Cyclotella meneghiniana Kützing, 1844	2,	cosm.
Bacillariophyceae	Cyclotella sp.	_, 1,	•••••
Bacillariophyceae	Surirella sp.	6,	
Bacillariophyceae	Svnedra sp.	1,8,	
Chlorophyceae	Ankistrodesmus bernardii Komárek, 1983	4,	circumtrop.
Chlorophyceae	Asterococcus sp.	4,	
Chlorophyceae	Botryococcus sp.	2,3,7,	
Chlorophyceae	Chlamydomonas sp.	1,	
Chlorophyceae	Chlorolobion (Ankistrodesmus) braunii (Nägeli) Komárek, 1979	4,	cosm.
Chiorophyceae	Chronologica (Thirdshoueshus) bruana (Pagen) Kollarek, 1979	ч,	coom.

(Continued)

Group	Species Names	Lake Number	Biogeography
Chlorophyceae	Chlorotetraedron incus (Teiling) Komárek & Kovácik, 1985	1,3,	cosm.
Chlorophyceae	Coelastrum indicum W.B. Turner, 1892	4,	tropicopol.
Chlorophyceae	Coelastrum pulchrum Schmidle, 1892	1,	
hlorophyceae	Coelastrum proboscideum Bohlin in Wittrock & Nordstedt, 1896	1,	cosm.
hlorophyceae	Coelastrum reticulatum (P.A. Dangeard) Senn, 1899	4,	cosm.
hlorophyceae	Coelastrum reticulatum var. cubanum Komárek, 1975	3,8,	circumtrop.
hlorophyceae	Coelastrum sphaericum Nägeli, 1849	3,	cosm.
hlorophyceae	Coenococcus sp.	4,7,8,	
hlorophyceae	Crucigenia tetrapedia W. West & G.S. West, 1902	2,	cosm.
hlorophyceae	Dictyosphaerium tetrachotomum var. fallax Komárek, 1983	3,	circumtrop.
hlorophyceae	Dictyosphaerium sp. 1	4,8,	
hlorophyceae	Dictyosphaerium sp. 2	1,	
Chlorophyceae	Golenkinia sp.	1,	
hlorophyceae	Kirchneriella dianae (Bohlin) Comas Gonzalez, 1980	1,3,4,	tropicopol.
hlorophyceae	Lagerheimia longiseta (Lemmermann) Printz, 1914	1,	cosm.?
hlorophyceae	Lauterborniella sp.	1,	
hlorophyceae	Monoraphidium contortum (Thuret)	1,2,8,	cosm.
	Komàrková-Legnerová, 1969		
hlorophyceae	Oocystis borgei J.Snow, 1903	2,	cosm.
hlorophyceae	Oocystis sp.	4,8,	
hlorophyceae	Pandorina morum (O.F. Müller) Bory de Saint-Vincent, 1824	4,	cosm.
hlorophyceae	Pediastrum duplex Meyen, 1829	1,2,5,	cosm.
hlorophyceae	Pediastrum duplex var. echinatum C.C. Jao, 1947	1,	cosm.?
hlorophyceae	Pediastrum simplex Meyen, 1829	3,	cosm.
hlorophyceae	Pediastrum tetras (Ehrenberg) Ralfs, 1844	1,2,4,8,	cosm.
hlorophyceae	Pseudodictyosphaerium elegans (Bachmann) Hindák, 1988	4,5,	cosm.
hlorophyceae	Scenedesmus acuminatus (Lagerheim) Chodat, 1902	1,2,	cosm.
Thlorophyceae	Scenedesmus armatus (R. Chodat) R. Chodat, 1913	1,	
Thlorophyceae	Scenedesmus brasiliensis Bohlin, 1897	2,	cosm.
Chlorophyceae	Scenedesmus opoliensis P.G. Richter, 1897	2,3,	cosm.
hlorophyceae	Scenedesmus tropicus W.B. Crow, 1923	1,	tropicopol.
hlorophyceae	Scenedesmus sp. 1	3,8,	
Chlorophyceae	Scenedesmus sp. 2	1,	
Chlorophyceae	Scourfieldia sp.	1,8,	
hlorophyceae	Sorastrum sp.	4,	
hlorophyceae	Tetraedron minimum (A.Braun) Hansgirg, 1888	1,8,	cosm.
Chlorophyceae	Tetrastrum staurogeniaeforme (Schröder) Lemmermann, 1900	1,7,	cosm.?
ygnematophyceae	Bambusina brebissonii Kützing, 1945	4,	cosm.
ygnematophyceae	Closterium dianae var. arcuatum (Brébisson ex Ralfs)	2,	cosm.
	Rabenhorst, 1868		
ygnematophyceae	Closterium ehrenbergii Meneghini ex Ralfs, 1848	4,	cosm.
ygnematophyceae	Closterium lineatum Ehrenberg ex Ralfs, 1848	4,	cosm.
ygnematophyceae	Closterium parvulum Nägeli, 1849	4,	cosm.
ygnematophyceae	Closterium ralfsii Brébisson ex. Brébisson in Ralfs, 1848	4,	cosm.
ygnematophyceae	Closterium setaceum Ehrenberg ex Ralfs, 1848	4,	cosm.
ygnematophyceae	Cosmarium binum Nordstedt in Wittrock & Nordstedt, 1880	4,	cosm.
ygnematophyceae	Cosmarium contractum var. minutum (Delponte) Coesel, 1989	1, 4, 8,	cosm.
vgnematophyceae	Cosmarium depressum (Nägeli) P.Lundell, 1871	1, 1, 0,	cosm.
vgnematophyceae	Cosmarium nudum (W.B. Turner) Gutwinski, 1902	4,	tropicopol.
ygnematophyceae	Cosmarium pygmaeum W.Archer, 1864	3,8,	cosm.
ygnematophyceae	Cosmarium quadrum var. sublatum (Nordstedt)	4,	cosm.
, o-ternate phycede	W. West & G.S. West, 1912	.,	
ygnematophyceae	Cosmarium spyridion W. West & G.S. West, 1895	1,4,	endemic?
ygnematophyceae	Cosmarium spyridion w. west & G.S. west, 1895	2,	endenne.
ygnematophyceae	Cosmarium sp. 2 Cosmarium sp. 3	2, 4,	endemic?
ygnematophyceae	Cylindrocystis sp.	ч, 1,2,	endenne.
ygnematophyceae	Euastrum didelta Ralfs ex Ralfs, 1848	4	cosm.
ygnematophyceae	Euastrum elegans var. madagascariense W. West & G.S. West, 1895	4	cosm.?
ygnematophyceae	Euastrum elegans val. madagascurense w. west & G.S. west, 1895 Euastrum humerosum Ralfs, 1848	4	cosm.
ygnematophyceae	Euastrum numerosum Kaijs, 1848 Euastrum praemorsum (Nordstedt) Schmidle, 1898	4 4,	cosm.
ygnematophyceae	Euastrum praemorsum (Nordstedt) Schnindie, 1898 Euastrum sp.	4, 1,4,5,	
ygnematophyceae	Gonatozygon sp. Micraetorias anomale Turner, 1802	4,	traniaanal
ygnematophyceae	Microsterias anomale Turner, 1892	4,	tropicopol.
ygnematophyceae	Micrasterias crux-melitensis (Ehrenberg) Hassall ex Ralfs, 1848	4,	cosm.
ygnematophyceae	Micrasterias decemdentata (Nägeli) W.Archer, 1861	4,	cosm.
ygnematophyceae	Micrasterias truncata var. africana F.E. Fritsch & M.F. Rich, 1924	4,	tropicopol.
Lygnematophyceae	Mougeotia sp.	4,	
Zygnematophyceae	Pleurotaenium ehrenbergii (Brébisson ex Ralfs) Delponte, 1878	4,	cosm.

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(Continued)

Group	Species Names	Lake Number	Biogeography
Zygnematophyceae Zygnematophyceae	Pleurotaenium ovatum Nordstedt, 1877 Pleurotaenium trabecula var. rectum (Delponte) W. West & G.S. West, 1904	4, 4,	tropicopol. cosm.
Zygnematophyceae	Staurastrum brachiatum Ralfs ex Ralfs, 1848	8,	cosm.
Lygnematophyceae	Staurastrum ceylanicum W. West & G.S. West, 1902	2,	orient.
ygnematophyceae	Staurastrum ellipticum West, 1892	-, 8,	cosm.
ygnematophyceae	Staurastrum gracile var. coronulatum Boldt, 1885	8,	cosm.
ygnematophyceae	Staurastrum inflexum Brébisson, 1856	4,	cosm.
ygnematophyceae	Staurastrum johnsonii W. West & G.S. West, 1896	1,	cosm.
vgnematophyceae	Staurastrum leptocladum Nordstedt, 1869	4,	tropicopol.
ygnematophyceae	Staurastrum muticum Brébisson ex Ralfs, 1848	2,7,	cosm.
ygnematophyceae	Staurastrum orbiculare var. ralfsii W. West & G.S. West, 1912	4,	cosm.
ygnematophyceae	Staurastrum sebaldi var. ornatum Nordstedt, 1873	8,	cosm.
ygnematophyceae	Staurastrum sp. 1	1,8,	
ygnematophyceae	Staurastrum sp. 2	1,7,	
ygnematophyceae	Staurastrum sp. 3	2,	
ygnematophyceae	Staurastrum sp. 4	1,7,	
ygnematophyceae	Staurastrum sp. 5	1,	
ygnematophyceae	Staurastrum subavicula (West) W. West & G.S. West, 1894	4,	cosm.
ygnematophyceae	Staurastrum tetracerum Ralfs ex Ralfs, 1848	1,3,8,	cosm.
ygnematophyceae	Staurodesmus dejectus (Brébisson) Teiling, 1967	1,	cosm.
ygnematophyceae	Staurodesmus sp. 1	3,	
ygnematophyceae	Staurodesmus sp. 2	1,	
uglenophyceae	Euglena sp. 1	5,	
uglenophyceae	Euglena sp. 2	4,5,	
uglenophyceae	Euglena acus (O.F.Müller) Ehrenberg, 1830	5,	
uglenophyceae	Phacus curvicauda Svirenko, 1915	3,4,	cosm.
uglenophyceae	Phacus sp.	5,	
uglenophyceae	Strombomonas sp.	4,	
uglenophyceae	Trachelomonas ĥorrida Palmer, 1905	4,	cosm.
uglenophyceae	Trachelomonas volvocina Ehrenberg, 1833	1,2,	cosm.
uglenophyceae	Trachelomonas sp.	3,4,5,7,8,	
lanthophyceae	Goniochloris fallax Fott, 1960	5,	cosm.?
lanthophyceae	Trochiscia sp.	3,	
lydrozoa	Hydra viridissima Pallas, 1766	4,	cosm.
lematoda	Achromadora micoletzkyi Stefanski, 1915	7,	cosm.
lematoda	Crocodorylaimus flavomaculatus (Linstow, 1876)	2,3,4,5,7,8,	cosm.
lematoda	Cryptonchus sp.	2, 7,	
lematoda	Dorylaimus cf. stagnalis Dujardin, 1845	7,	cosm.
lematoda	Eumonhystera cf. gerlachi (Meyl, 1954)	5,	Europe
lematoda	Ironus ignavus Bastian, 1865	7,	cosm.
lematoda	Ironus tenuicaudatus De Man, 1876	2,7,8,	palaearct., afrotrop., orient.
lematoda	Mesodoryilaimus cf. subtiloides (Paetzold, 1958)	2,5,7,	Europe
ematoda	Mesodorylaimus sp. 1	2,	
ematoda	Mesodorylaimus sp. 2	2,	
lematoda	Monhystera cf. paludicola De Man, 1881	8,	cosm.
lematoda	Monhystrella cf. paramacrura (Meyl, 1953)	7, 8,	palaearct., afrotrop., orient.
lematoda	Mononchus cf. aquaticus Coetzee, 1968		cosm.
lematoda	Mylonchulus lacustris (Cobb, 1915)	2,3,7,	palaearct., afrotrop., orient., nearct neotrop.
lematoda	Neoactinolaimus duplicidentatus (Andrássy, 1968)	2,3,7,	palaearct., afrotrop.
lematoda	Neotobrilus longus (Leidy, 1852)	7,	palaearct., afrotrop., orient., nearct., neotrop.
lematoda	Oncholaimus cf. oxyuris Ditlevsen, 1911	7,	brackish water
ematoda	Plectus cf. pusillus Cobb, 1893	7,	palaearct., afrotrop., austral., nearct., neotrop.
lematoda	Prodorylaimus sp.	7, 2, 5,	-
ematoda	Rhabdolaimus aquaticus De Man, 1880	2,	cosm.
ematoda	Rhabdolaimus terrestris De Man, 1880	5,	cosm.
lematoda	Species 1	5,	
ematoda	Tobrilus helveticus (Hofmänner, 1914)	2,4,5,7,	palaearct.
otifera	Anuraeopsis fissa Gosse, 1851	1,5,6,8,	cosm.
otifera	Anuraeopsis navicula Rousselet, 1911	2,3,8,	cosm.
otifera	Asplanchna cf. brightwellii Gosse, 1850	3,	cosm.
otifera	Brachionus angularis Gosse, 1851	1,3,8,	cosm.
otifera	Brachionus falcatus Zacharias, 1898	1,2,5,6,7,8,	cosm.
otifera	Brachionus quadridentatus Hermann, 1783	3,7,8,	cosm.
otifera	<i>Cephalodella</i> sp.	8,	

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Group	Species Names	Lake Number	Biogeography
Rotifera	<i>Colurella</i> sp.	7,	
otifera	Conochilus sp.	7.	
otifera	Dicranophorus tegillus Harring & Myers, 1928	4, 5,	nearc., orient.
otifera	Epiphanes cf. clavulata (Ehrenberg, 1831)	5,	cosm.
otifera	Euchlanis sp.	4,	
otifera	Filinia opoliensis (Zacharias, 1898)	7,8,	cosm.
otifera	Lepadella (H.) ehrenbergi (Perty, 1850)	7,	cosm.
otifera	Hexarthra intermedia Wiszniewski, 1929	1,5,7,8,	cosm.
otifera	Keratella procurva (Thorpe, 1891)	6,7,	cosm.? (excl. nearct.)
otifera	Keratella valga (Ehrenberg, 1834)	2,8,	cosm.
otifera	Lecane curvicornis (Murray, 1913)	4,5,	cosm.
otifera	Lecane bulla (Gosse, 1851)	4,5,7,8,	cosm.
otifera	Lecane aculeate (Jakubski, 1912)	3,4,5,6,	cosm.
otifera	Lecane closterocerca (Schmarda, 1859)	5,7,	cosm.
otifera	Lecane furcata (Murray, 1913)	4,7,8,	cosm.
otifera otifera	Lecane hamata (Stokes, 1896)	4,5,6,7,	cosm.
	Lecane hornemanni (Ehrenberg, 1834) Lecane inermis (Bryce, 1892)	2,3,	cosm.
otifera	Lecane inopinata Harring & Myers, 1926	3,4,5,7,	cosm.
tifera tifera		7,	cosm.
otifera	Lecane luna (Müller, 1776)	4,8, 2,	cosm.
otifera	Lecane lunaris (Ehrenberg, 1832) Lecane nana (Murray, 1913)	2, 4,	cosm.
otifera	Lecane pyriformis (Daday, 1915)	4, 4,6,7,	cosm.
otifera	Lecane quadridentata Ehrenberg, 1830	4,0,7, 4,	cosm. cosm.
otifera	Lecane cf. ruttneri Hauer, 1938	4, 6,	afrotr., orient., neotr.
otifera	Lecane signifera (Voigt, 1902)	0, 4,	cosm.
otifera	Lecane thienemanni (Hauer, 1938)	6,	afrotrop., orient., austr., neotr.
otifera	Lecane unquitata (Fadeew, 1925)	0, 4,7,	eastern hemisphere
otifera	Lecane spp.	4, 7, 4,	eastern nennsphere
otifera	Levane spp. Lepadella patella (Müller, 1773)	2,4,7,	cosm.
otifera	Lepadella sp.	5,	cosiii.
otifera	Lepadella quinquecostata (Lucks, 1912)	4,	cosm.
otifera	Macrochaetus collinsii (Gosse, 1867)	4,	cosm.
otifera	Mytilina ventralis (Ehrenberg, 1832)	4,7,	cosm.
otifera	Mytilina sp.	4,7,	cosiii.
otifera	Platyias leloupi Gillard, 1957	4,5,	pres. cosm. (excl. palaearct.)
otifera	Polyarthra indica Segers & Babu, 1999	5,6,	afrotrop., orient., pacific
otifera	Polyarthra vulgaris Carlin, 1943	1,3,	cosm.
otifera	Polyarthra sp.	4,5,	coshi.
otifera	Scaridium sp.	4,	
otifera	Testudinella incisa (Ternetz, 1892)	3,8,	cosm.
otifera	<i>Testudinella patina</i> (Hermann, 1783)	4,5,8,	cosm.
otifera	Trichocerca cf. pusilla (Jennings, 1903)	1,3,	cosm.
otifera	Trichocerca chattoni (De Beauchamp, 1907)	1,5,	cosm.
otifera	Trichocerca cf. rattus (Müller, 1776)	5,6,	cosm.
otifera	Trichocerca similis (Wierzejski, 1893)	1,	cosm.
otifera	Trichocerca tigris (Müller, 1786)		cosm.
otifera	Trichocerca sp.	4, 2,5,8,	coshi.
otifera	Trichotria tetractis (Ehrenberg, 1830)	2,5,6,	cosm.
igochaeta	Dero (Aulophorus) hymanae Naidu, 1962	2, 3,	Southern India
igochaeta	Chaetogaster crystallinus Vejdovsky, 1883	3, 7,	palaearct., afrotrop., orient., nearct.
igochaeta	Nais africana Brinkhurst, 1966	7,8,	afrotrop.
igochaeta	Nais grieda Dimensio, 1900 Nais pseudoobtusa Piguet, 1906	3,	palaearct., afrotrop., orient., nearct., neotrop.
igochaeta	Nais simplex Piguet, 1906	3,7,	palaearct., afrotrop., orient., nearct.
igochaeta	Nais sp. 1	3,	endemic?
gochaeta	Nais sp. 2	3,	
gochaeta	Nais sp. 3	3.	
igochaeta	Pristina aequiseta Bourne, 1891	3, 7,	cosm.
igochaeta	Pristina proboscidea Beddard, 1896	7,	palaearct., orient., austral., neotrop
igochaeta	Vejdovskyella comata (Vejdovsky, 1883)	3,	palaearct., afrotrop., orient., nearct
rudinea	Alboglossiphonia heteroclita (Linnaeus, 1761)	3, 7,	palaearct., nearct.
pepoda	Elaphoidella bidens (Schmeil, 1894)	3,8,	cosm.
pepoda	Elaphoidella grandidieri Guerne & Richard, 1893	3,	afrotrop., orient., pacific, neotr.
pepoda	Elaphoidella sp.	4,8,	
pepoda	Epactophanes richardi Mrazek, 1893		cosm.
pepoda	Cryptocyclops linjanticus (Kiefer, 1928)	7, 4,5,	afrotrop., orient., holarct. (aralo-caspian and mediterranear

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Group	Species Names	Lake Number	Biogeography
Copepoda	Ectocyclops hirsutus (Kiefer, 1930)	4,	afrotrop.
Copepoda	Mesocyclops insulensis Dussart, 1982	8,	endemic
Copepoda	Mesocyclops pilosus (Kiefer, 1930)	1,2,3,7,8,	endemic
Copepoda	Microcyclops cf. varicans (Sars, 1863)	3,4,5,7,	cosm.
Copepoda	Paracyclops sp.	7,8,	Genus cosmopolitan
Copepoda	Thermocyclops cf. crassus (Fischer, 1853)	5,	cosm.
Copepoda	Thermocyclops decipiens (Kiefer, 1929)	1,4,	cosm.
Copepoda	Thermocyclops neglectus (Sars, 1909)	6,	afrotrop.
Copepoda	Tropocyclops cf. tenellus (Sars, 1909) sensu Lindberg (1952)	8,	afrotrop., endemic?
Copepoda	Tropodiaptomus (Anadiaptomus) madagascariensis poseidon Brehm, 1952	2,7,	endemic
Cladocera	Alona cambouei Guerne & Richard, 1893	4,7,	circumtrop., eastern hemisphere
Cladocera	Alona guttata Sars, 1862	8,	cosm., species group
Cladocera	Anthalona harti harti Van Damme, Sinev & Dumont, 2011	4,7,	afrotrop.
Cladocera	Ceriodaphnia cornuta Sars, 1885	2,4,	tropicopol.
Cladocera	Ceriodaphnia laticaudata P.E. Müller, 1867	4,	cosm.
Cladocera	Chydorus sphaericus (O.F. Müller, 1785)	4,	cosm., species group
Cladocera	Daphnia laevis Birge, 1879	2,7,8,	tropicopol.; North, South America and Africa only
Cladocera	Dunhevedia serrata Daday, 1898	4,5,	tropicopol.
Cladocera	Euryalona orientalis (Daday, 1898)	4,	tropicopol.
Cladocera	Ilyocryptus spinifer Herrik, 1882	5,8,	tropicopol.
Cladocera	Karualona socotrana Dumont & Silva-Briano, 2000		afrotrop., Sokotra
Cladocera	Kurzia longirostris (Daday, 1898)	5, 5, 2,	circumtrop., eastern hemisphere
Cladocera	Leberis diaphanus (King, 1853)	2,	circumtrop., eastern hemisphere
Cladocera	Macrothrix spinosa King, 1853	3,4,5,	tropicopol.
Cladocera	Moinodaphnia macleavi (King, 1853)	4,	torpicopol.
Cladocera	Notoalona globulosa (Daday, 1898)	5,	circumtrop.
Ostracoda	Cryptocandona sp.	2,	palaearct, introduced?
Ostracoda	Cypretta cf. seurati Gauthier, 1929	4,	palaerct., neotrop., orient., pacific
Ostracoda	Cypria cf. lenticularis G.W. Müller, 1898	7,	afrotrop.
Ostracoda	Cyprididae <i>Gen.</i> sp.	8,	1
Ostracoda	Gomphocythere obtusata Sars, 1910	7,8,	afrotrop.
Ostracoda	Nealecypris obtusa (Klie, 1933)	1,4,	afrotrop.
Ostracoda	Potamocypris sp.	2,	L.
Ostracoda	Zonocypris costata (Vávra, 1897)	2,7,	palaearct., afrotrop.
Acari	Tactocepheus cf. velatus (Michael, 1880)	2,	cosm.
Acari	Trhypochtoniellus longisetus (Berlese) f. setosus Willmann, 1928	2,	cosm.
Acari	Punctoribates sp.	3,	