Relationships of stream algal community structure to catchment deforestation in eastern Madagascar

Rebecca J. Bixby[1]

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

Jonathan P. Benstead[2]

Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487 USA

Michael M. Douglas[3]

*Centre for Tropical Wetlands Management, Charles Darwin University,
Darwin, Northern Territories 0909 Australia*

Catherine M. Pringle[4]

Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA

Abstract. Approximately 0.5 million km of tropical stream channel are modified by catchment deforestation annually, but the consequences of this process for community structure are poorly understood because of a dearth of data from tropical regions. We compared the algal communities of epilithic biofilms from 3 tropical rainforest streams draining Ranomafana National Park (RNP) in eastern Madagascar and 3 open-canopy streams draining RNP's deforested peripheral zone. Forest and open-canopy streams differed in canopy cover and mean water temperature but did not differ in substrate composition or major nutrient chemistry. We recorded 137 algal taxa, of which ~45% can be considered endemic or potentially endemic. Deforestation had significant effects on algal community structure. Complete separation between forest and open-canopy streams was observed in nonmetric multidimensional scaling ordinations based on species cell densities, species presence–absence, and cell densities of algal growth forms. Forest streams were characterized by higher species richness and cell densities of motile and solitary growth forms (e.g., *Navicula* spp.) than were open canopy streams. Open-canopy streams had more variable community structure than forest streams and were characterized by prostrate and solitary (e.g., *Planothidium* spp.) and chain-forming/ stalked growth forms (e.g., *Gomphonema* spp.). Community shifts and reductions in species richness observed in open-canopy streams show that diatom biodiversity might be affected adversely by vegetation removal in the catchments we studied. Given that Madagascar has lost most of its rainforest in recent centuries, it is reasonable to assume that historical deforestation has led to shifts in algal assemblages at broader regional scales. Our results also suggest that global algal diversity could be affected by tropical deforestation if similar patterns of endemism and alteration of algal assemblages occur in the 0.5 million km of stream channel affected by tropical deforestation annually.

Key words: tropical streams, deforestation, algae, diatoms, endemism, Madagascar, PRIMER.

Stream ecosystems are tightly linked to their catchments through terrestrial vegetation (Ross 1963, Hynes 1975, Wallace et al. 1997). One component of this linkage is the strong relationship between catchment vegetation and the structure of stream biofilm communities (complex assemblages of algae, bacteria, fungi, and meiofauna growing on submerged surfaces; Lock et al. 1984). For example, removal of canopy vegetation typically is associated with changes in algal community structure within biofilms (Hansmann and Phinney 1973, Lowe et al. 1986, Naymik et al. 2005). Such structural shifts are caused, in part, by the

[1] E-mail addresses: bbixby@unm.edu
[2] jbenstead@bama.ua.edu
[3] michael.douglas@cdu.edu.au
[4] cpringle@uga.edu

varying sensitivity of benthic algal taxa to quantity and quality of ambient light (DeNicola et al. 1992, Tuji 2000). Alteration of catchment vegetation also can affect nutrient delivery and ratios (Likens et al. 1970, Neill et al. 2001), which have potential effects on algal populations (Shortreed and Stockner 1983, Lowe et al. 1986, Hill and Knight 1988).

Scientific understanding of the effects of vegetation removal (i.e., deforestation) on stream communities is based largely on studies of relatively well understood stream systems in temperate regions—areas that also are undergoing net afforestation (FAO 2001). In stark contrast, current estimates of tropical deforestation rates are ~1.4×10^5 km^2/y (during 1990–2000; FAO 2001). At this rate of forest removal, >0.5 million km of tropical stream channel are affected by deforestation annually (assuming a drainage density of 4 km/km^2; Benstead et al. 2003b), which probably causes fundamental transformations of community structure and ecosystem-level function. However, relatively little is known about stream ecosystems or of the ecological consequences of catchment deforestation in tropical regions (Benstead et al. 2003a, Benstead and Pringle 2004).

The structure of stream biofilm communities in the tropics and their responses to forest removal might be expected to differ from biofilm community structure and responses in temperate regions because of biogeographic and climatic factors (e.g., higher irradiance and temperature) or biotic factors directly related to climate (e.g., constant canopy cover and litterfall from evergreen rainforest; Covich 1988). Unfortunately, data on tropical biofilm community structure are rare (Archibald 1972, Mpawenayo and Mathooko 2005). Species richness is particularly poorly understood, and traditional concepts of cosmopolitanism are increasingly giving way to appreciation of potentially high rates of endemism, particularly in the Southern Hemisphere (Kilroy et al. 2007, Vyverman et al. 2007). Data describing how these poorly understood communities respond to habitat transformation are virtually nonexistent. We are aware of no tropical studies that have investigated the effects of deforestation on algal species assemblages, including changes in cell densities and physiognomies.

Given the current dramatic rate of transformation of tropical stream ecosystems caused by catchment deforestation, a pressing need exists for greater understanding of the effects of catchment deforestation on structural characteristics of tropical stream communities. Here, we use multivariate analysis of algal community data from 3 streams that drain protected tropical rainforest in eastern Madagascar and 3 streams that drain nearby deforested catchments to ask 2 questions: 1) What is the structure of forest stream algal communities in eastern Madagascar? and 2) How is this community structure affected by catchment deforestation?

Methods

Study sites

Our study was conducted within Ranomafana National Park (RNP; lat 21°15′S, long 47°27′E) and its peripheral zone. RNP is a 41,300-ha reserve located in eastern Madagascar. The park spans elevations of 400 to 1500 m asl, and its vegetation consists of primary and secondary lowland and premontane tropical rainforest. The peripheral zone is a buffer area, extending 3 km from the park boundary, in which land use consists of swidden (slash-and-burn) agriculture, secondary (fallow) vegetation, riparian rice paddies, and remnant forest patches. Mean monthly precipitation in the region varies seasonally and can be extremely high (e.g., 14–1171 mm, September 1992–June 1994; Balko 1998).

Six streams were used in our study (Table 1); 3 were within the forest protected by RNP, whereas 3 were in deforested areas within or near the peripheral zone (hereafter referred to as open-canopy streams). All streams were small to medium sized (5.3–13.7 m mean width), 700 to 1100 m asl, and had fast-flowing water with gravel, cobble, and boulder substrata (Table 1). Mean canopy cover differed greatly between the 2 stream types (forest streams: 71–83%, open-canopy streams: 0–14%; Table 1). Concurrent studies showed that forest and open-canopy streams did not differ with respect to sediment cover or dominant substrate types (Benstead et al. 2003b). Nutrient concentrations also did not differ greatly between the 2 stream types. Ranges in mean concentrations of [NO$_3$+NO$_2$]-N and NH$_4$-N were 46 to 72 µg/L and 6 to 36 µg/L, respectively, during 1997 through 1999 (Benstead et al. 2003b). Concentrations of soluble reactive P were consistently below detection limits (<6.8 µg/L) in all 6 streams (Benstead et al. 2003b). All study streams flow into the River Namorona, a 5th-order river with seasonal flows that peak in February and March (Chaperon et al. 1993).

Algal community structure

All fieldwork was conducted during a period of stable discharge in the dry season (April–May 1999). Algal communities were sampled from representative cobbles ($n = 3$) collected from riffles in each of the 6 streams. Cobble surfaces were scrubbed with a stiff

Table 1. Physical description of streams sampled in Ranomafana National Park and peripheral zone, eastern Madagascar, April–May 1999.

Stream	Mean width (m)	Mean maximum depth (m)	Mean temperature (°C)	Mean conductivity (µS/cm)	Substratum	Mean canopy cover (%)	Catchment land use
Forest							
Mariavaratra (MAR)	6.0	0.31	17.0	14.7	Cobble, with boulders and gravel/sand	71	Selectively logged during mid-1980s
Fompohonona (FOM)	5.3	0.38	17.0	20.5	Cobble with sand and boulders	74	Primary forest, some selective logging
Vatoharanana (VAT)	9.6	0.51	17.0	15.3	Boulders, cobble, and sand	83	Primary forest, some human disturbance
Open-canopy							
Tomaro (TOM)	13.7	0.72	18.5	12.6	Cobble	0	Rice agriculture
Tolongoina (TOL)	7.2	0.56	17.3	13.6	Boulders, cobble, gravel, and sand	14	Rice and sugar cane agriculture
Menarano (MEN)	9.7	0.48	17.5	13.6	Cobble and sand	0	Rice and cassava agriculture

toothbrush and rinsed with a wash bottle. Periphyton slurries were preserved immediately in 5% formalin.

Algal community composition was characterized from quantitative subsamples of randomly selected slurries from the cobble replicates. Densities and growth forms of filamentous cyanobacteria, filamentous red algae, and unicellular green algae were determined with a Palmer–Maloney counting chamber at 400× magnification (brightfield optics) on a Zeiss Universal research microscope (Carl Zeiss, Jena, Germany). Taxa were identified and enumerated along a transect(s) until 500 cells/units were recorded. Some cyanobacterial filaments were counted in 10-µm lengths (1 length = 1 unit). In samples with extremely low cell densities, a maximum of 10 transects was examined.

To determine diatom densities, 2-mL aliquots were heated with 20 mL of 30% H_2O_2 for 1 h and rinsed 6 times with distilled water to remove oxidation by-products. Processed subsamples were evaporated onto coverslips and mounted to microscope slides with Naphrax® (Brunel Microscopes Ltd., Chippenham, Wiltshire, UK) mounting medium to make permanent slides. Specimens along transects were examined under oil immersion at 1000× magnification using brightfield optics. Five hundred valves were enumerated from each sample. In samples that had extremely low diatom densities, a maximum of 10 transects was examined. Identification of taxa was based on taxonomic literature, including work from Madagascar (Lenoble and Manguin 1949, Manguin 1952, Spaulding and Kociolek 1998, Metzeltin and Lange-Bertalot 2002).

Growth forms were classified into 18 functional groups (based on algal physiognomies, personal observations, and published literature; Hoaglund et al. 1982, Round et al. 1990, Metzeltin and Lange-Bertalot 2002) nested within 3 broad categories of general vertical position within the 3-dimensional community (attached, lower canopy, upper canopy).

Multivariate analyses of algal communities

Four multivariate techniques were used to examine possible differences in algal community structure between stream types (forest and open-canopy): 1) analysis of similarities, 2) index of multivariate dispersion, 3) similarity percentages, and 4) nonmetric multidimensional scaling ordinations. Analyses were done with the ANOSIM, MVDISP, SIMPER, and MDS routines, respectively, in the PRIMER software application (version 6; Plymouth Marine Labs, Plymouth, UK; Clarke and Warwick 2001). First, a dissimilarity matrix was generated by comparing the entire algal

composition of all sample pairs. Intersample compositional similarities were computed with the Bray–Curtis coefficient (Bray and Curtis 1957), which has been shown to have the most robust relationship with ecological distance when compared with several commonly used dissimilarity coefficients (Faith et al. 1987). Dissimilarity matrices were derived for 4 data sets: presence–absence data for all algal species, untransformed cell densities for all algal species, untransformed cell densities for the 7 species that contributed the most to the differences between stream types (identified by SIMPER; see below), and total cell densities for the 18 growth-form categories. The degree of multivariate correlation between the untransformed species data and the other data sets was tested with the RELATE routine in PRIMER (Clarke and Warwick 2001), which performs the equivalent of a nonparametric Mantel test using the Spearman rank correlation.

We used 2-way nested ANOSIM to compare the average rank similarities of samples between the 2 stream types, with replicate streams nested within stream type. ANOSIM calculates a test statistic, the R-statistic, which varies between 0 and 1; high values indicate differences between stream types (i.e., forest and open-canopy streams). A test of the significance of the R-statistic is obtained by comparing its value to a distribution of values expected under the null hypothesis of no difference between treatments (Clarke and Warwick 2001). This nonparametric permutation test was used in preference to comparable parametric tests, such as multivariate analysis of variance, because the latter are based on assumptions (e.g., that abundances follow a multivariate normal distribution) unlikely to be satisfied for most multispecies data sets (Clarke and Warwick 2001). The limited number of permutations available for the test of stream type ($n = 3$ replicates for each stream type) meant that it was not possible to determine the significance of R-statistic values at probabilities <10%. ANOSIM was done on both untransformed cell density and presence–absence data to distinguish between the influence of species richness and compositional differences on community structure.

Second, an index of multivariate dispersion (IMD; Clarke and Warwick 2001) was calculated for each stream type to determine whether community structure was more variable in open-canopy or forest streams. This index describes differing dispersion across groups based on similarity within groups.

Third, the % contributions of each taxon or growth form to the overall dissimilarity ($\overline{D}i$) between stream types was quantified by the SIMPER routine (Clarke and Warwick 2001). This procedure also calculates the ratio of the mean $\overline{D}i$ for all sample pairs between groups to the standard deviation (SD) (mean $\overline{D}i$/SD [$\overline{D}i$]). This ratio indicates how consistently a taxon or growth form contributes to mean dissimilarity across all pairs within a group and is a measure of the importance of each taxon or growth form in discriminating communities between groups (Clarke and Warwick 2001).

Last, the ordination technique of nonmetric multidimensional scaling (NMDS) was used to provide a graphical summary of the relationships in the similarity matrices described above (Clarke and Warwick 2001). NMDS ordination is considered a robust form of ordination for ecological analyses (Clarke and Warwick 2001). To aid in interpretation of patterns in the ordination, bubble plots were used to show trends in species cell densities in each sample for the taxa or growth forms that were important in differentiating between stream types.

To test further for differences between forest and open-canopy streams, 2-way analyses of variance (Statistica, version 5; StatSoft, Tulsa, Oklahoma), were done on the species and growth form densities identified by SIMPER analyses as important in discriminating between stream types.

Results

Differences between stream types

One hundred thirty-seven algal taxa were recorded from the 6 streams (Appendix). Approximately 45% of these taxa are endemic or potentially endemic to Madagascar. Algal community structure was significantly different among replicate streams (i.e., within a stream type) for both presence–absence data (R-statistic = 0.56, $p = 0.01$) and cell density data (R-statistic = 0.56, $p = 0.01$). Despite these differences among individual streams, the ordination plots showed clear separation of samples from forest and open-canopy streams for both the presence–absence data (Fig. 1A) and untransformed species density data (Fig. 1B). This observation was supported by the high ANOSIM R-statistic values for the tests between stream types based on the presence–absence data (R-statistic = 0.48, $p = 0.1$) and cell density data (R-statistic = 0.82, $p = 0.1$). The clear separation between stream types based on presence–absence data indicates that the difference in algal communities was not simply the result of differences in relative abundance, but also was caused by differences in species richness. Species richness generally was higher in forest streams than in open-canopy streams. Based on species cell density data, community similarity was lower among open-canopy streams than among forest streams (27% vs
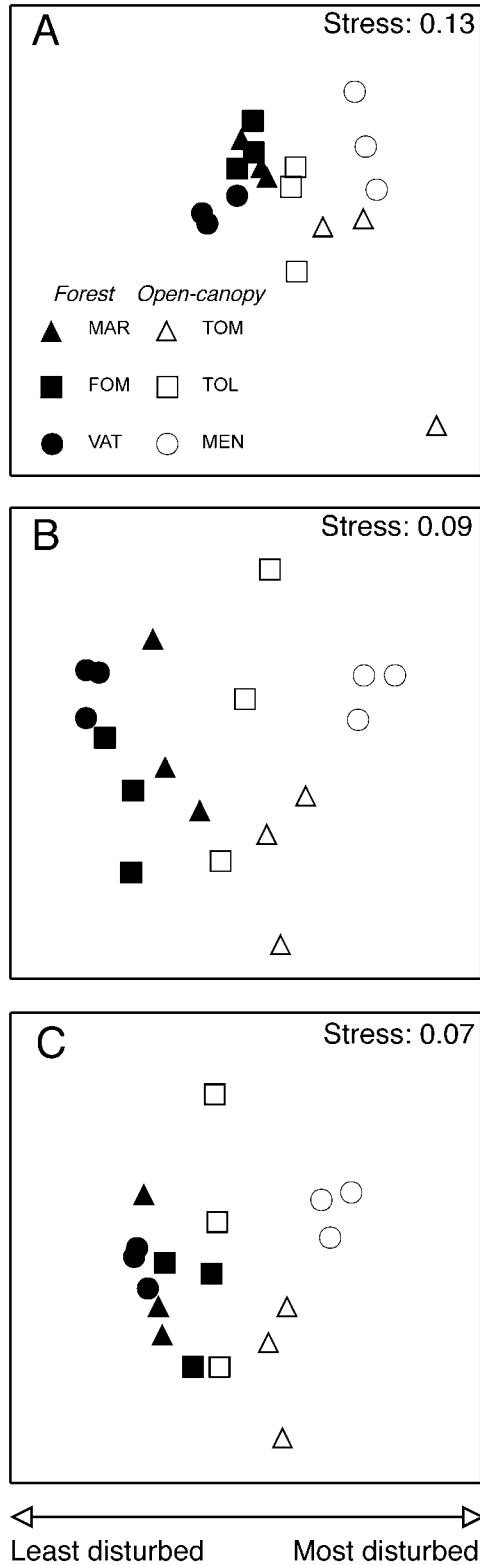
FIG. 1. Nonmetric multidimensional scaling ordination plot of algal communities from forest and open-canopy streams in eastern Madagascar based on Bray–Curtis dissimilarities and presence–absence-transformed data (A), untransformed species cell density data (B), and untransformed cell densities of functional groups (based on growth form) (C). See Table 1 for stream abbreviations.

39%). IMD values also indicated a much more variable community structure in open-canopy than in forest streams based on presence–absence (open-canopy IMD = 1.3, forest IMD = 0.7) and species cell density (open canopy IMD = 1.2, forest IMD = 0.8) (Fig. 1A, B). All other analyses were done on the species cell density data because it was highly correlated with the presence–absence data ($\rho = 0.96$; $p = 0.001$) and gave the lowest stress in a 2-dimensional ordination.

Differences in species cell densities between stream types

Overall, 36 species accounted for a total of 90% of the overall dissimilarity between open-canopy and forest streams. Seven of these taxa contributed >3% to between-group dissimilarity, and together they accounted for 60% of the difference between stream types. Two species, *Gomphonema* cf. *evanescens* Spaulding and Kociolek and *Eolimna* cf. *minima* (Grun.) Lange-Bert., contributed 23.3% and 15.5%, respectively (Table 2). The similarity matrix derived from just these 7 species was highly correlated with the similarity matrix based on all species ($\rho = 0.96$; $p = 0.001$), a result that indicates the strong contribution of these 7 species to the overall pattern between stream types. Most of these 7 species occurred in higher abundance in the open-canopy streams. Only 2 species, *E.* cf. *minima* and *Achnanthes subhudsonis* Hust., were found in higher abundance in forest streams (Table 2, Fig. 2A–G). Mean densities of *A. subhudsonis* were significantly higher in forest than in open-canopy streams ($F_{1,4} = 16.1$, $p = 0.02$), and mean densities of *G.* cf. *evanescens* were significantly higher in open-canopy than in forest streams ($F_{1,4} = 22.2$, $p = 0.009$). Of these 7 species, *G.* cf. *evanescens* was the best indicator of stream type and had consistently higher densities in open-canopy than in forest streams, whereas *Gomphonema spauldingae* Metzeltin and Lange-Bert. had the most variable cell densities among streams and was the poorest indicator of stream type (Table 2).

Differences in growth forms between stream types

Differences between stream types also were apparent when data were aggregated into growth-form categories. The similarity matrix based on growth forms was highly correlated with the similarity matrix based on species densities ($\rho = 0.93$, $p = 0.01$) and showed clear separation between open-canopy and forest streams (Fig. 1C). This interpretation was

TABLE 2.   Mean (± SE) cell density (cells/mm^2) of the algal taxa that contributed ≥3% to the overall dissimilarity between forest and open-canopy streams. $\overline{D}i$ is the % contribution of each taxon to the overall dissimilarity between the 2 stream types; $\overline{D}i$/SD($\overline{D}i$) is the ratio of the mean $\overline{D}i$ for all sample pairs between stream types to the standard deviation of $\overline{D}i$ and is a measure of the importance of each taxon in discriminating communities between stream types.

Taxon	Forest Cell density	Agriculture Cell density	Forest vs open-canopy %$\overline{D}i$	$\overline{D}i$/SD($\overline{D}i$)
Forest taxa				
Eolimma cf. *minima*	27.8 ± 6.8	17.1 ± 13.2	15.5	1.1
Achnanthes subhudsonis	7.3 ± 1.6	1.0 ± 0.9	4.2	1.1
Open-canopy taxa				
Gomphonema cf. *evanescens*	1.2 ± 0.5	60.0 ± 15.9	23.3	1.4
Gomphonema spauldingae	0.7 ± 0.5	17.6 ± 10.6	5.8	0.7
Navicula cf. *cryptotenella*	6.8 ± 2.8	11.7 ± 6.6	4.3	1.1
Planothidium jacobii	4.6 ± 1.5	9.9 ± 5.3	3.5	1.0
Planothidium lanceolatum	2.7 ± 1.5	10.5 ± 6.4	3.3	1.1

supported by the moderately high ANOSIM *R*-statistic (*R*-statistic= 0.48, $p = 0.1$) and high average dissimilarity between stream types (73%). Five growth forms each contributed >5% to the dissimilarity between stream types and together they accounted for 88% (Table 3). Three of these growth forms—mucilage stalks attached to substrate, motile and solitary, and prostrate and solitary—were particularly reliable indicators of stream type, and together they contributed >75% of the total dissimilarity between stream types (Table 3). All growth forms except motile and solitary had higher mean densities in open-canopy than in forest streams (Table 3, Fig. 3A–E). This difference was significant only for the mucilage stalks attached to substrate growth form ($F_{1,4} = 14.5$, $p = 0.02$).

Discussion

Community responses to changes in canopy cover

Overall, algal community structure responded clearly to differences in canopy cover between stream types. Multivariate analyses illustrated broad community separation between open-canopy and forest streams and detailed responses to a gradient in % canopy cover among streams. For example, the algal community in the open-canopy stream with the most intact riparian cover (Tolongoina [TOL]; 14% cover) was most similar to the algal community in forest streams (Table 1, Fig. 1A–C). The ordinations also discriminated accurately among streams on the basis of the various levels of historical disturbance in their catchments. For example, the least disturbed catchment (Vatoharanana [VAT]) had experienced limited tree removal (mostly for honey collection; Benstead 2001), and its algal community was the most dissimilar from the communities in the open-canopy streams

(Table 1). The other 2 forest streams underwent some selective harvest before RNP was established (Benstead 2001) and were relatively more similar in algal community structure to open-canopy streams than was the VAT site. The ordinations also reflected levels of historical disturbance in open-canopy streams (i.e., Menarano [MEN] > TOM > TOL). The MEN site was geographically most distant from currently forested areas and perhaps was the stream most transformed by the effects of deforestation; it also had an algal community that was most dissimilar from the algal communities in forest streams.

Macroinvertebrate community structure in these 6 streams was analyzed using similar multivariate techniques to those used to analyze algal communities in our study (Benstead et al. 2003b). Macroinvertebrate communities also differed markedly between forest and open-canopy streams. The macroinvertebrate community in the partial-canopy site (TOL) was more similar (and MEN was least similar) to that of the 3 forest streams. However, ordinations based on macroinvertebrate data did not reflect the relative level of disturbance of forest stream catchments (Benstead et al. 2003b). Algal communities appeared to be more sensitive to historical disturbance of riparian (or catchment) vegetation than were macroinvertebrate communities. This result is similar to those of other studies, in which algal populations have been shown to respond with greater sensitivity (i.e., shifts in dominant taxa) to cumulative physical consequences of vegetation removal (especially increases in light; Naymik et al. 2005).

Algal data from the 6 streams showed a marked community shift from an assemblage dominated by smaller prostrate diatom taxa in forest streams to a physically more complex community dominated by larger prostrate and chain-forming/stalked diatom
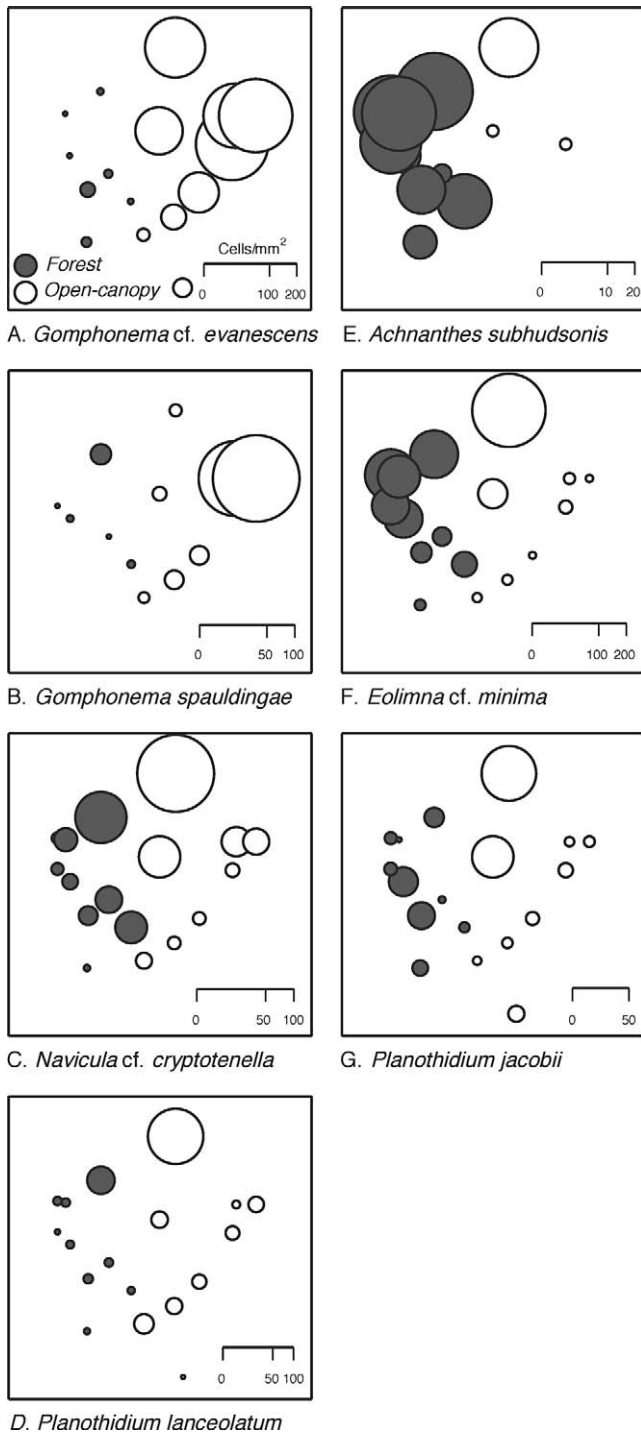
FIG. 2. Nonmetric multidimensional scaling ordination plot based on untransformed cell densities of each algal species (Fig. 1B) that contributed ≥3% to the overall dissimilarity between forest and open-canopy streams. The diameter of each circle is proportional to density. Scales are shown in the lower right corner of each plot. A.—*Gomphonema* cf. *evanescens*. B.—*Gomphonema spauldingae*. C.—*Navicula* cf. *cryptotenella*. D.—*Planothidium lanceolatum*. E.—*Achnanthes subhudsonis*. F.—*Eolimna* cf. *minima*. G.—*Planothidium jacobii*.

taxa in the open-canopy streams. In the forest streams, vertical development was restricted by light limitation, and prostrate taxa (e.g., *A. subhudsonis*) were dominant. Open-canopy streams had higher irradiance as a result of deforestation, which enabled the algal community to develop vertically and to show complexity in growth form. Taxa with larger cells (e.g., *Planothidium* spp.) and chain-forming/stalked taxa (e.g., *Gomphonema* spp.) in the upper canopy have a competitive advantage over shaded understory taxa (Hoaglund et al. 1982, Hill and Knight 1988). These patterns indicate that light is the dominant driver that shapes differences in algal community composition and growth forms among our 6 streams.

Increased community complexity, indicated by multiple growth forms, also was reflected in the variability among replicates in open-canopy streams. Physically more complex communities with local intracommunity shading (Hoaglund et al. 1982) coupled with microhabitat patchiness (related to differences in substrate, light availability, flow, and nutrient availability at the microhabitat scale; Pringle et al. 1988) probably caused the increased variability among replicates in open-canopy streams.

In some temperate streams, canopy removal results in both increased light levels and increased nutrient concentrations from watershed erosion (Hansmann and Phinney 1973, Naymik et al. 2005). Combined increases in irradiance and nutrients can result in taxonomic shifts from diatoms to primarily filamentous algae (Lowe et al. 1986, Rosemond and Brawley 1996). However, differences in algal communities between the forest and open-canopy streams in our study primarily were related to shifts among dominant diatom taxa. No pronounced shift to a filamentous algae-dominated community that could be associated with a higher-light, higher-nutrient environment was observed. In our study, nutrient concentrations were similarly low between forest and open-canopy streams and might have been limiting to many filamentous algal taxa (Borchardt 1996).

Comparisons of algal biomass and communities in tropical streams of Madagascar with those of their temperate stream counterparts show both similar and dissimilar patterns related to irradiance and riparian canopy cover. Overall, low irradiance limits algal biomass in both tropical (i.e., Mosisch et al. 2001) and temperate (i.e., Hill and Knight 1988, Greenwood and Rosemond 2005) systems. However, this trend did not hold true in our study, in which algal biomass (i.e., biovolume; data not shown) was low and not significantly different between forested and open-canopy streams. However, whether this similarity in algal biomass between stream types was caused by

Table 3. Mean ($\pm$ SE) cell density (cells/mm^2) of algal growth forms that contributed $\geq 5\%$ to the overall dissimilarity between forest and open-canopy streams. $\overline{Di}$ is the % contribution of each growth form to the overall dissimilarity between stream types; $\overline{Di}/$ SD($\overline{Di}$) is the ratio of $\overline{Di}$ for all sample pairs between stream types to the standard deviation of $\overline{Di}$ and is a measure of the importance of each growth form in discriminating communities between stream types.

	Forest	Agriculture	Forest vs open-canopy	
Growth forms	Cell density	Cell density	%$\overline{Di}$	$\overline{Di}$/SD($\overline{Di}$)
"Forest" growth forms				
Motile and solitary	43.3 $\pm$ 11.0	38.6 $\pm$ 26.0	25.9	1.3
"Open-canopy" growth forms				
Mucilage stalks attached to substrate	2.2 $\pm$ 0.6	86.6 $\pm$ 28.4	36.6	1.3
Prostrate and solitary	22.5 $\pm$ 4.2	31.4 $\pm$ 18.4	12.0	1.4
Filamentous	5.9 $\pm$ 3.6	16.1 $\pm$ 8.1	8.4	0.9
Mostly solitary (some chain-forming)	2.9 $\pm$ 1.8	24.3 $\pm$ 22.5	5.1	0.6

nutrient limitation, high grazing, or other factors, is not known.

Few data are available to compare algal community responses to irradiance in tropical vs temperate streams. In general, as light increases, species composition in both ecosystem types shift to include greater numbers of larger-celled or stalked algal taxa, growth forms that might have a competitive advantage for light acquisition (Hoaglund et al. 1982, Hudon and Bourget 1983). In the tropical streams in our study, continuous canopy cover in the forest streams and, conversely, high irradiances in the open-canopy streams, might drive key differences in species composition among communities. Species richness in our forest streams was high compared to that of temperate forest streams (i.e., Greenwood and Rosemond 2005). The aseasonality of evergreen tropical forest provides constant low-light conditions in the forest streams. Therefore, greater numbers of taxa might be photo-adapted to high riparian canopy cover (Hill 1996) in tropical forest streams than in seasonally shaded temperate forest streams.

Biodiversity and endemism

Biodiversity and degree of endemism typically are higher on tropical continental islands, such as Madagascar, than in temperate regions (Goodman and Benstead 2005). This pattern might be especially true for microorganisms, such as algae (Spaulding and Kociolek 2003), which have been poorly investigated compared to vascular plants and vertebrates. In general, tropical algal biodiversity and taxonomy are inadequately understood (Mann and Droop 1996), but the few studies done in tropical regions to date all have demonstrated a high degree of algal endemism (Hustedt 1949, Coste and Ricard 1982, Foged 1986, Moser et al. 1998). Madagascar has been isolated biogeographically for a long enough time (>80 million

y) to allow speciation and adaptive radiation in many taxonomic groups. Several examples exist of Malagasy diatom species flocks (closely related taxa) that presumably are a result of this long isolation (e.g., *Actinella* and *Gomphonema*; Kociolek et al. 1997, Spaulding and Kociolek 1998). More than 80% of Madagascar's algal taxa described to date might be endemic (Metzeltin and Lange-Bertalot 2002, Spaulding and Kociolek 2003). This figure is consistent with that observed for other plant and animal groups (Goodman and Benstead 2005). Five of the 7 dominant diatom taxa, and many of the less common taxa reported in our study, probably are endemic to Madagascar and new to science.

Algae in Madagascar's streams also have a high diversity of morphological adaptations. For example, the endemic *Achnanthes gondwana* Metzeltin and Lange-Bertalot (a species commonly recorded in our study) has a unique morphological adaptation for colony formation (a spine-like structure on 1 valve attaches to a siliceous ridge on an adjacent valve; Metzeltin and Lange-Bertalot 2002). In addition, most *Gomphonema* taxa in our study streams belong to a species flock that has no isolated stigma, a perforation in the cell wall that is morphologically characteristic of most *Gomphonema* taxa (Spaulding and Kociolek 1998). These astigmate *Gomphonema* also possess a uniquely structured, siliceous axial plate that differentiates this closely related Malagasy group from other *Gomphonema* (Spaulding and Kociolek 1998). These examples of unique morphological characters further illustrate the results of Madagascar's long geographic isolation.

In conclusion, our analysis revealed large differences in algal community structure between 3 forest streams and 3 open-canopy streams in eastern Madagascar. Algal community structure, based on species presence, species cell densities, and growth forms, was significantly different between stream types, with lower species richness in open-canopy streams. The commu-
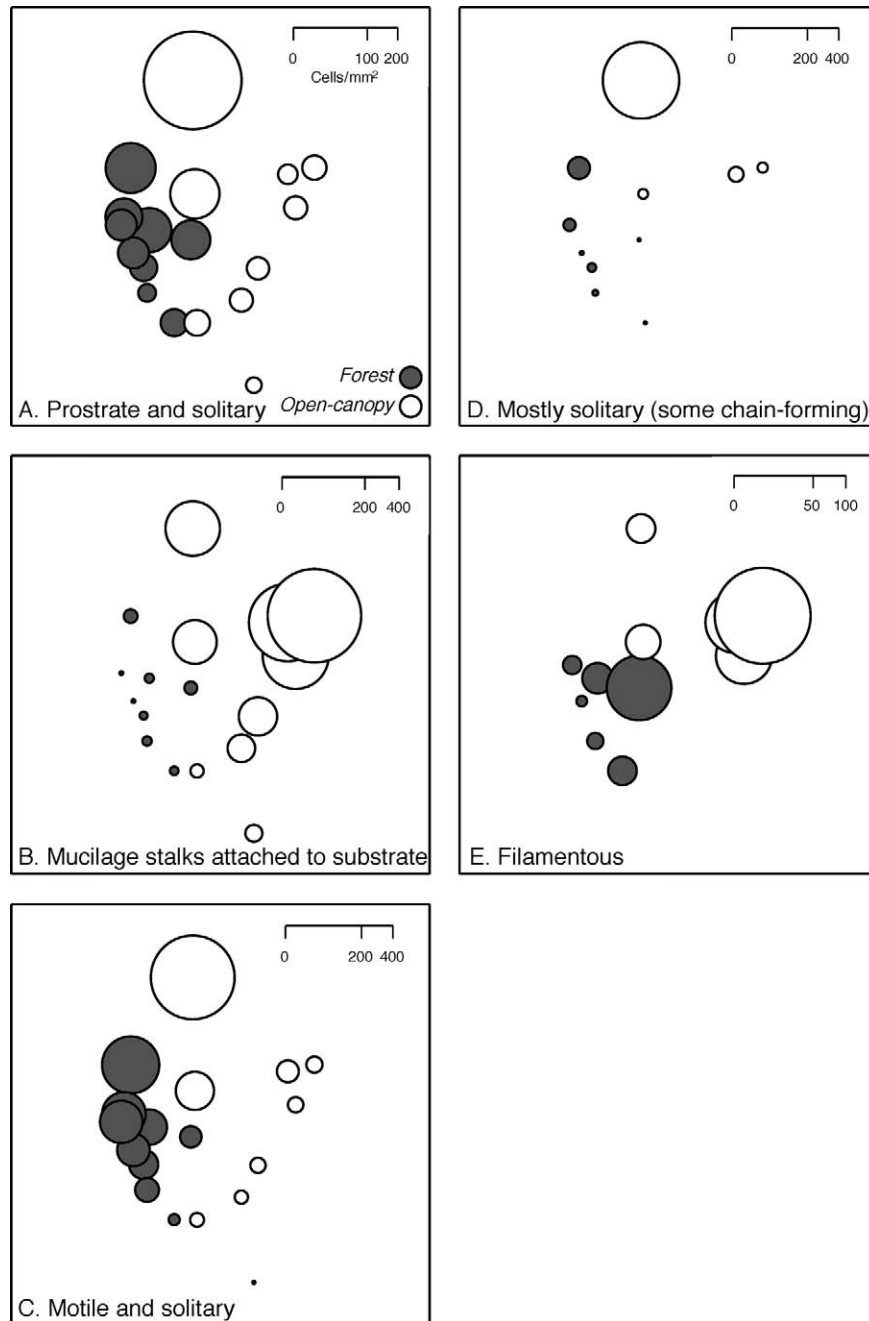
FIG. 3. Nonmetric multidimensional scaling ordination plot based on untransformed cell densities of each algal growth form (Fig. 1C) that contributed ≥5% to the overall dissimilarity between forest and open-canopy streams. Diameter of each circle is proportional to density. Scales are shown in the upper right corner of each plot. A.—Prostrate and solitary. B.—Mucilage stalks attached to substrate or in chains. C.—Motile and solitary. D.—Mostly solitary (some forming chain-like colonies). E.—Filamentous.

nity shifts and reductions in species richness related to deforestation observed in our study show that diatom diversity might be affected adversely by vegetation removal in the catchments we studied. Given that Madagascar has lost ≥63% of its rainforest in recent centuries (Green and Sussman 1990), it is reasonable to assume that historical deforestation has led to shifts in

stream algal communities on large regional scales. Such changes, when considered in light of the high proportion of endemic taxa found in our study, suggest that global algal diversity could be affected by deforestation in tropical regions, such as Madagascar. Such effects of deforestation are well documented for larger organisms (Goodman and Benstead 2003),

but equivalent data for microbial communities are still extremely rare. However, similar transformations of algal community structure might be common to the 0.5 million km of stream channel affected by tropical deforestation annually (Benstead et al. 2003b).

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APPENDIX. List of algal taxa sampled from forest and agriculture streams in Ranomafana National Park and its peripheral zone, eastern Madagascar, April to May 1999.

Taxon	Growth form
Achnanthes gondwana Metzeltin & Lange-Bert.	Adnate and colonial
Achnanthes inflata (Kütz.) Grun.	Adnate and solitary
Achnanthes linearis (W. Smith) Grun.	Adnate and solitary
Achnanthes sp. 1	Adnate and solitary
Achnanthes sp. 2	Adnate and solitary
Achnanthes sp. 3	Adnate and solitary
Achnanthes sp. 4	Adnate and solitary
Achnanthes sp. 5	Adnate and solitary
Achnanthes sp. 6	Adnate and solitary
Achnanthes sp. 7	Adnate and solitary
Achnanthes subatomoides (Hust.) Lange-Bert. & Archibald	Adnate and solitary
Achnanthes subhudsonis Hust.	Adnate and solitary
Achnanthidium exiguum var. *constricta* (Torka) Hust.	Adnate and solitary
Achnanthidium macrocephalum (Hust.) Bukht. & Round	Adnate and solitary
Achnanthidium minutissimum (Kütz.) Czarn.	Adnate and solitary
Amphora sp.	Solitary
Caloneis elongata Bourrelly & Manguin	Motile and solitary
Caloneis fontinalis (Grun.) Lange-Bert. & Reichardt in Lange-Bert. & Metzeltin	Motile and solitary
Cocconeis placentula var. *euglypta* (Ehrenb.) Grun.	Adnate and solitary
Cocconeis sp.	Adnate and solitary
Diadesmis arcuata (Heiden) Lange-Bert.	Motile and solitary/colonial
Diadesmis cf. *corrugata* Lange-Bert.	Motile and solitary
Diadesmis cf. *lacunosa* Lange-Bert. in Moser et al.	Motile and solitary
Diadesmis contenta (Grun.) D.G. Mann in Round et al.	Motile and solitary
Diploneis elliptica (Kütz.) Cl.	Motile and solitary
Encyonema minutum (Hilse *ex* Rabenh.) D.G. Mann in Round et al.	Solitary or forming mucilage stalks
Encyonema neogracile Krammer	Solitary or forming mucilage stalks
Encyonema silesiacum (Bleisch *ex* Rabenh.) D.G. Mann in Round et al.	Solitary or forming mucilage stalks
Encyonema sp. 1	Solitary or forming mucilage stalks
Encyonema sp. 2	Solitary or forming mucilage stalks
Encyonema sp. 3	Solitary or forming mucilage stalks
Eolimna cf. *minima* (Grun.) Lange-Bert.	Solitary and motile
Eunotia incisa W. Smith	Adnate and solitary
Eunotia naegelii Migula	Adnate and solitary
Eunotia rhomboidea Hust.	Adnate and solitary
Eunotia siolii Hust.	Adnate and solitary
Eunotia sp. 1	Adnate and solitary
Eunotia sp. 2	Adnate and solitary
Eunotia veneris (Kütz.) DeToni	Adnate and solitary
Fallacia insociabilis (Krasske) D.G. Mann in Round et al.	Motile and solitary
Fragilaria vaucheriae (Kütz.) J.B. Peterson	Solitary or short chains
Frustulia cf. *rhomboides* (Ehrenb.) DeToni	Motile and solitary
Frustulia cf. *saxonica* Ehrenb.	Motile and solitary
Frustulia crassiundosa Metzeltin & Lange-Bert.	Motile and solitary
Frustulia rhomboides (Ehr.) DeToni	Motile and solitary
Frustulia saxonica Ehrenb.	Motile and solitary
Frustulia viridula (Bréb.) DeToni	Motile and solitary
Gomphonema cf. *evanescens* Spaulding & Kociolek	Chain-forming or stalked
Gomphonema cf. *gracile* Ehrenb. emend VanHeurck	Chain-forming or stalked
Gomphonema cf. *innocens* Reichardt	Chain-forming or stalked
Gomphonema cf. *puvillum* Spaulding & Kociolek	Chain-forming or stalked
Gomphonema eurycephalus Spaulding & Kociolek	Chain-forming or stalked
Gomphonema lagenula Kütz.	Chain-forming or stalked
Gomphonema parvulum (Kütz.) Kütz.	Chain-forming or stalked
Gomphonema perinsignis Spaulding & Kociolek	Chain-forming or stalked
Gomphonema sp. 2	Chain-forming or stalked
Gomphonema sp. 3	Chain-forming or stalked
Gomphonema sp. 4	Chain-forming or stalked
Gomphonema sp. 5	Chain-forming or stalked

Appendix. Continued.

Taxon	Growth form
Gomphonema sp. 7	Chain-forming or stalked
Gomphonema sp. 8	Chain-forming or stalked
Gomphonema sp. 9	Chain-forming or stalked
Gomphonema sp. 10	Chain-forming or stalked
Gomphonema sp. 12	Chain-forming or stalked
Gomphonema spauldingae Metzeltin & Lange-Bert.	Chain-forming or stalked
Luticola cf. *mitigata* (Hust.) D.G. Mann	Solitary and motile
Luticola mitigata (Hust.) D.G. Mann	Solitary and motile
Luticola muticoides (Hust.) D.G. Mann	Solitary and motile
Melosira varians C. Agardh	Filaments of 1–4 cells
Navicula angusta Grun.	Solitary and motile
Navicula arvensis Hust.	Solitary and motile
Navicula cf. *angusta* Grun.	Solitary and motile
Navicula cf. *cryptotenella* Lange-Bert.	Solitary and motile
Navicula cf. *horstii* Metzeltin	Solitary and motile
Navicula cf. *leistikowii* Lange-Bert.	Solitary and motile
Navicula cf. *radiosa* Kütz.	Solitary and motile
Navicula cf. *subtilissima* Cl.	Solitary and motile
Navicula cf. *trivialis* Lange-Bert.	Solitary and motile
Navicula cf. *viridula* (Kütz.) Ehrenb.	Solitary and motile
Navicula cryptocephala Kütz.	Solitary and motile
Navicula cryptotenella Lange-Bert.	Solitary and motile
Navicula difficillima Hust.	Solitary and motile
Navicula heimansii Van Dam and Kooyman	Solitary and motile
Navicula radiosa Kütz.	Solitary and motile
Navicula soehrensis Krasske	Solitary and motile
Navicula sp. 1	Solitary and motile
Navicula sp. 4	Solitary and motile
Navicula sp. 5	Solitary and motile
Navicula sp. 7	Solitary and motile
Navicula sp. 8	Solitary and motile
Navicula sp. 9	Solitary and motile
Navicula sp. 10	Solitary and motile
Navicula sp. 11	Solitary and motile
Navicula sp. 12	Solitary and motile
Navicula sp. 13	Solitary and motile
Navicula sp. 14	Solitary and motile
Navicula sp. 15	Solitary and motile
Navicula sp. 16	Solitary and motile
Navicula sp. 17	Solitary and motile
Navicula sp. 18	Solitary and motile
Navicula sp. 19	Solitary and motile
Neidium sp.	Solitary and motile
Nitzschia acicularis (Kütz.) W. Smith	Mostly solitary (some chain-like colonies)
Nitzschia capitellata Hust.	Mostly solitary (some chain-like colonies)
Nitzschia dissipata (Kütz.) Grun.	Mostly solitary (some chain-like colonies)
Nitzschia palea (Kütz.) W. Smith	Mostly solitary (some chain-like colonies)
Nitzschia sp. 1	Mostly solitary (some chain-like colonies)
Nitzschia sp. 2	Mostly solitary (some chain-like colonies)
Nitzschia sp. 3	Mostly solitary (some chain-like colonies)
Nupela praecipua Reichardt	Adnate and solitary
Nupela schoemaniana Lange-Bert.	Adnate and solitary
Planothidium biporomum (Hohn & Hellerman) Lange-Bert.	Adnate and solitary
Planothidium jacobii (Manguin) Metzeltin & Lange-Bert.	Adnate and solitary
Planothidium lanceolatum (Bréb.) Round & Bukht.	Adnate and solitary
Planothidium miotum (Carter) Lange-Bert.	Adnate and solitary
Rhopalodia gibberula (Ehrenb.) O. Müller	Solitary
Sellaphora pupula (Kütz.) Mereschk.	Motile and solitary
Sellaphora seminulum (Grun.) D.G. Mann	Motile and solitary
Stauroneis anceps Ehrenb.	Motile and solitary
Stauroneis resoluta Moser, Lange-Bert. & Metzeltin	Motile and solitary

APPENDIX. Continued.

Taxon	Growth form
Stenopterobia delicatissima (Lewis) Van Heurck	Motile and solitary
Surirella sp.	Motile and solitary
Synedra cf. *acus* Kütz.	Solitary and upright
Synedra goulardi Bréb.	Solitary and upright or in chains
Synedra rumpens Kütz.	Solitary and upright or in chains
Synedra ulna (Nitzsch) Ehrenb.	Solitary and upright
Anabaena sp.	Filamentous
Audouinella sp.	Filamentous
Batrachospermum sp.	Filamentous
Chamaesiphon sp.	Single cell
Chroococcus sp.	Single cell
Closterium sp.	Single cell
Cosmarium sp.	Single cell
Lyngbya sp. 1	Filamentous
Lyngbya sp. 2	Filamentous
Netrium sp.	Single cell
Oscillatoria sp.	Filamentous