

Where Are We Now Regarding Hawaiian Stream Algal Systematics? (A Suspiciously Cosmopolitan Flora)

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Abstract

The last decade has witnessed a great advancement in our understanding of the Hawaiian stream algal flora. Several large surveys have produced comprehensive data sets for the four largest main Hawaiian islands (Kaua'i, O'ahu, Maui, and Hawai'i), which have resulted in a substantial increase of recorded taxa for the state. A compiled checklist is presented for the stream algal flora of Hawai'i, which includes 174 taxa. Overall, the Hawaiian stream algal flora is estimated to be only 2.3% endemic, which is very low compared to other groups of organisms in the state. The major drawback of most stream algal studies to date has been the reliance upon morphology-based identification techniques. As a result, most Hawaiian stream algal collections have had taxonomic names "force fit" to them from floras based on other geographical regions around the world. This has led to the recognition of a largely cosmopolitan Hawaiian stream algal flora with a very low rate of endemism, compared to other groups of organisms. Although it is recognized that the stream algal flora may indeed be more cosmopolitan than other groups of organisms in Hawai'i due to its high dispersal capability, the current estimate is regarded as suspiciously high. Artificial deflation of the degree of endemism may have arisen from a combination of "force-fitting" names from other regional floras, a reliance on morphological characters for identification, and a lack of taxonomic expertise. Estimates of the degree of endemism in the Hawaiian stream algal flora will likely increase with the inclusion of molecular- and genome-based characters in future taxonomic studies.

Introduction

"Across the world there is a prevailing view that freshwater algae are cosmopolitan. The notion has seldom been tested and is unlikely to be true in genetic terms....The degree of endemism is probably masked by the 'force-fitting' of European names..." (Tyler, 1996, p.127)

Freshwater algae are largely viewed as cosmopolitan in their geographic distribution (Tyler, 1996). A number of inseparable factors likely contribute to this impression. First, since floristic works are only available for a limited number of geographical regions, phycologists have relied heavily on available floras as opposed to developing concepts of new taxa for each new area explored. For example, the most comprehensive sources of cyanobacterial taxonomy are based on the European flora, yet are used worldwide (e.g., Geitler, 1932; Anagnostidis & Komárek, 1985). Second, most phycologists still rely almost exclusively on morphological characters for routine identifications, especially for ecological studies that require the identification of many collections, and the use of these characters may lead to an underestimate of genetic diversity. This is especially true for algae that have very simple morphologies, with few defining characters (e.g., the crustose red alga, *Hildenbrandia* [Sherwood & Sheath, 2003]). Third, the paucity of well-trained taxonomists in the current generation leaves the door open for misidentification and over-reliance on the small number of available floras. These factors have all likely played a role in our understanding of the stream algal flora of the Hawaiian Islands and resulted in a floristic checklist that is comprised almost exclusively of cosmopolitan species, or at least those known to inhabit a broad tropical or subtropical range of geographical regions.

The evolutionary breadth of organismal life contained under the informal classification of “algae” can be misleading in some cases. Although a completely satisfactory definition for algae does not exist, in general they include photosynthetic organisms that are not members of the green plant lineage. Algae thus contain members of two of the three domains of life (Eubacteria and Eukaryota), and within the eukaryotes encompass a wide variety of quite distinct evolutionary lines. It should be recognized that the comparisons and statistics presented in the current paper are representative of an incredibly wide lineage diversity – a case which does not exist (to this degree) for any other group of organisms included in this symposium.

The first written records of Hawaiian stream algae were published approximately 130 years ago. The earliest known record dates back to Nordstedt (1876) on collections of freshwater algae and charophytes (henceforth included within the freshwater algae) from an expeditionary report to the islands. Since then, a number of papers have dealt with various aspects of the Hawaiian stream algal flora, from ecological perspectives of these primary producers (LaPerriere, 1995; Chong, 1996) to diatom (Fungladda *et al.*, 1983) and macroalgal taxonomy (Vis *et al.*, 1994; Filkin *et al.*, 2003), and phenology and phylogenetics of red algae (Sherwood *et al.*, 2004). A bibliographic checklist summarizing the non-marine algal records from Hawai‘i was recently published (Sherwood, 2004) and included indications of the endemic versus non-endemic elements of the flora.

One of the most challenging questions regarding Hawaiian freshwater algae is the determination of the native flora, which is virtually impossible for several reasons. The historical records of freshwater algae in Hawai‘i are patchy, and a very incomplete picture is available prior to the first Polynesian settlements (between 400–1100 AD) and European contact (1778 AD) (Zeigler, 2002). Additionally, freshwater algae played a very minor ethnobotanical role in the diet of early Hawaiians (Abbott, 1984), and thus cultural records of the stream algal flora are also lacking. Another factor is that the earliest identifications (from 1876 onward) were by researchers working with identification resources developed for vastly different regions of the world. Given this, how close can we come to determining the native stream algal flora of the Hawaiian Islands? Two different approaches are available: algae in relatively pristine areas could be assumed to represent the native flora, or molecular tools could be used to assess the degree of divergence with respect to representatives in other areas (Sherwood, 2006). However, it will be almost, if not entirely impossible to discover what the original floristic composition was, as it is almost certain that alterations occurred following human settlement to the islands (Sherwood, 2006).

The present paper is a summary and critical assessment of the Hawaiian stream algal literature. Trends are presented from published reports of stream algae in Hawai‘i. An emphasis is placed on how the future use of molecular characters may influence our understanding of the origins and the level of endemism of the Hawaiian stream algal flora.

Materials and Methods

Summary of previously published literature

Stream algae records from previously published literature reports were gathered and summarized. The list includes only peer-reviewed publications, or those currently under review in the primary literature. Only records from stream habitats are included (i.e., this analysis excludes standing water habitats such as taro patches, reservoirs, fish ponds, and other brackish-water areas). However, much of the older literature combines records from a variety of habitats under a single category, and these could not be separated in the current analysis. The list is largely derived from the stream algal records contained in Sherwood (2004), with the addition of recent literature (Sherwood, 2006). Only the soft algae are included in the present analysis (i.e. the diatoms are excluded). Both microalgae (those algae requiring light microscopy for visualization of the entire algal thallus) and macroalgae (benthic algae with a thallus construction visible to the naked eye) are included in the comparative list. Taxa endemic to the Hawaiian Islands are marked with an asterisk.

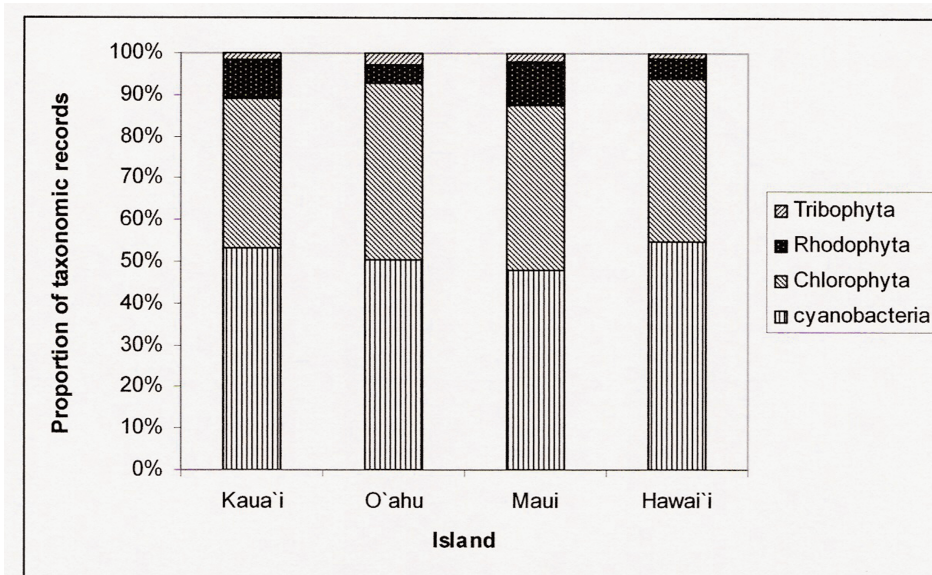


Figure 1. The proportion of stream algae records from each of the four main Hawaiian Islands belonging to each broad taxonomic category (cyanobacteria, Chlorophyta, Rhodophyta and Tribophyta).

Analyses of published records

Taxonomic records were sorted by broad taxonomic category: cyanobacteria (or “blue-green algae”), Chlorophyta (green algae), Rhodophyta (red algae), Dinophyta (dinoflagellates), Chrysophyta (chrysophytes), and Tribophyta (yellow-green algae or xanthophytes), and compared across islands to determine if similar proportions of taxa from each category were identified from each island. The Chrysophyta and Dinophyta were excluded from the analysis since only a single taxon was identified from each group. Similarly, only records from the four main Hawaiian Islands were included in the analysis since these were the only islands for which enough data were available to make meaningful comparisons. A similar analysis previously presented for stream macroalgae of the Hawaiian Islands (Sherwood, 2006) allows a comparison between the macroalgal stream algal flora and the entire stream algal flora.

Published molecular analyses of a broad taxonomic range of freshwater algae were evaluated for reported levels of genetic divergence across different geographical regions. These data were used to explore the implications of including molecular or genetic data for re-interpretation of the taxonomy of the algal groups included in the current study.

Results and Discussion

Summary of the Hawaiian stream algal flora

The non-diatom component of the stream algal flora of the Hawaiian Islands is comprised of an estimated 174 taxa, including 83 cyanobacteria, 77 Chlorophyta, 7 Rhodophyta, 1 Dinophyta, 1 Chrysophyta, and 5 Tribophyta (Table 1). These records were drawn from a total of 22 literature reports, ranging in publication date from the late 1800's (Nordstedt, 1876) to the present (Sherwood, 2006). Of these 174 taxa, only four, or 2.3% of the total, are believed to be endemic to the Hawaiian Islands. This value is extremely low when compared to the estimate of 5.0% for the entire non-marine algal flora (Sherwood, 2004), not to mention the estimated values for the marine red algal

Table 1. Stream algal taxa, including both macroalgae and microalgae, recorded in the literature for the Hawaiian Islands. Taxa believed to be endemic to Hawai'i are indicated with an asterisk (*). Island names are abbreviated as follows: L = Laysan Island, Ni = Ni'ihau, K = Kaua'i, O = O'ahu, Mo = Moloka'i, M = Maui and H = Hawai'i. Reference numbers correspond with those in the Literature Cited section.

Taxon	Distribution	References
Cyanobacteria		
<i>Anabaena catenula</i> (Kütz.) Bornet et Flahault	K, O	7, 9, 19
<i>Anabaena</i> sp.	O	8, 12, 17
<i>Aphanothece naegelii</i> Wartm. ex Rabenh.	O	7, 8, 9, 17, 18, 19
<i>Calothrix braunii</i> (A. Br.) Bornet et Flahault	M, H	12
<i>C. fusca</i> (Kütz.) Bornet et Flahault	M	6, 7, 9, 12, 19
<i>Chamaesiphon elongatus</i> (Nordst.) Kann syn. <i>C. curvatus</i> var. <i>elongatum</i> Nordst.	K, O	6, 10, 13
<i>Cylindrospermum catenatum</i> Ralfs	O	7, 9, 19
<i>C. stagnale</i> (Kütz.) Bornet et Flahault	K, O, H	3, 7, 9, 12, 19
<i>Cylindrospermum</i> sp.	K, O, M, H	3, 8, 10, 12, 17
<i>Dichothrix baueriana</i> (Grun.) Bornet et Flahault	M	12
<i>Fischerella ambigua</i> (Nägeli) Gomont	O	7, 8, 9, 19
<i>Geitlerinema splendidum</i> (Grev. ex Gom.) Anagn.	O, H	3, 12
<i>Gloeocapsa magna</i> (Bréb.) Komárek et Anagn.	O, H	6, 7, 8, 9, 10, 19
<i>G. polydermatica</i> Kütz.	O, H	7, 9, 19
<i>G. quarternata</i> Kütz.	O, H	7, 8, 9, 17, 18, 19
<i>Heteroleibleinia distincta</i> (Schmidle) Anagn. et Komárek syn. <i>Lyngbya distincta</i> (Nordst.) Schmidle	O, H	7, 9, 19
<i>Hydrocoleum meneghinianum</i> Kütz.	H	11, 12
<i>Leptolyngbya angustissima</i> (W. West et G.S. West) Anagn. et Komárek	O	3, 12
<i>L. foveolarum</i> (Mont. ex Gomont) Anagn. et Komárek	O	11, 12
<i>L. tenuis</i> (Gomont) Anagn. et Komárek syn. <i>Phormidium tenue</i> (Menegh.) Gomont	K, M	13, 15, 20
* <i>Lyngbya cladophorae</i> Tilden	O, H	7, 9, 19
<i>L. major</i> Menegh.	O	12
<i>L. martensiana</i> Menegh.	O, H	7, 9, 18, 19
<i>Lyngbya</i> sp.	O, H	8, 17
<i>Microchaete uberrima</i> N. Carter	K	3, 12
<i>Microcoleus lacustris</i> (Rabenh.) Farl.	O, H	3, 12, 15
<i>M. vaginatus</i> (Vaucher) Gom.	O, H	2
<i>Nostoc commune</i> Vaucher	O	6, 7, 9, 12, 17, 18, 19
<i>N. foliaceum</i> Moug.	O, H	7, 9, 18, 19
<i>N. linckia</i> (Roth) Bornet ex Bornet et Thur. syn. <i>N. piscinale</i> Kütz.	K, O	3, 6, 7, 9, 12, 19
<i>N. paludosum</i> Kütz.	M, H	6, 7, 9, 12, 19
<i>N. pruniforme</i> C. Ag.	K, O, M, H	11, 12
<i>N. verrucosum</i> (L.) Vaucher	O, M, H	7, 9, 12, 17, 18, 19
<i>Nostochopsis lobatus</i> Wood emend. Geitler	K, O, M	3, 12
<i>N. radians</i> Bharadwaja	K, O	3, 12
<i>Oscillatoria limosa</i> C. Agardh ex Gom.	K, O, H	3, 12
<i>O. princeps</i> Vauch. ex Gom.	H	12
<i>O. sancta</i> Kütz.	K, O, H	7, 8, 9, 12, 18, 19
<i>O. subbrevis</i> Schmidle	K	12
<i>Oscillatoria</i> sp.	K, O, H	3, 8, 10, 17
<i>Phormidium ambiguum</i> Gomont	K, M	11, 12
<i>P. amoenum</i> (Kütz. ex Gomont) Anagn. et Komárek	K	3, 12
<i>P. autumnale</i> C. Ag. ex Gom.	M	12
<i>P. corium</i> (C. Agardh) Gomont syn. <i>P. papyraceum</i> Gomont	K, O	3, 7, 8, 9, 12, 18, 19
<i>P. favosum</i> Gomont	O	7, 9, 18, 19

Table 1 (continued)

Taxon	Distribution	References
<i>P. formosum</i> (Bory ex Gomont) Anagn. et Komárek syn. <i>Oscillatoria formosa</i> Bory	O, H	7, 8, 9, 12, 19
<i>P. inundatum</i> Kütz.	K, O, M, H	12, 20
<i>P. pachydermaticum</i> Frémy	M	12
<i>P. putealis</i> (Mont. ex Gomont) Anagn. et Komárek	H	12
<i>P. retzii</i> (C.Agardh) Gomont	K, O, M, H	2, 3, 12, 13, 16, 20
<i>P. splendidum</i> (Grev. ex Gomont) Anagn. et Komárek syn. <i>Oscillatoria splendida</i> Grev.	O, H	3, 19
<i>P. stagninum</i> C.B.Rao	O	11, 12
<i>P. subfuscum</i> Kütz.	K, O, M	12, 20
<i>P. subincrustatum</i> Fritsch et Rich	O, H	11, 12
<i>P. tinctorium</i> Kütz.	K, O	11, 12
<i>P. truncicola</i> Ghose	K, O	12
<i>Phormidium</i> spp.	K, O, M, H	8, 10, 12, 17
<i>Planktothrix planctonica</i> (Elekin) Anagn. et Komárek syn. <i>Microcoleus lyngbyaceus</i> (Kütz.) P.L.Crouan et H.M.Crouan	L, K, H	2
<i>Pseudanabaena</i> sp.	O	3, 12
<i>Rivularia haematites</i> (DC.) C.Agardh	K, H	12, 20
<i>R. minutula</i> (Kütz.) Born. et Flah.	K, H	12
<i>Schizothrix calcicola</i> (C.Agardh) Gomont	Ni, K, O, M, H	2
<i>S. friesii</i> (C.Agardh) Gomont	K, O, M, Mo, H	2, 20
<i>S. lacustris</i> A.Braun ex Gomont	K	20
<i>S. rivulis</i> (Wolle) F.E.Drouet	K, H	12, 13
<i>Scytonema arcangelii</i> Bornet et Flahault	O, M, H	12, 20
<i>S. chiasmum</i> Geitler	K	3, 12
<i>S. coactile</i> Mont. ex Kütz.	K	3, 12
<i>S. crispum</i> (C.Agardh) Bornet	K, O, M, H	6, 7, 9, 10, 12, 16, 18, 19
<i>S. fritschii</i> S.L.Ghose	H	12, 15
<i>S. guyanese</i> (Mont.) Bornet et Flahault	O	6, 7, 9, 19
<i>S. myochrous</i> (Dillwyn) C.Agardh	O, M	20
<i>S. ocellatum</i> Lyngb.	O	6, 7, 8, 9, 19
<i>S. rivulare</i> Borzi	O, M	7, 8, 9, 12, 18, 19
<i>S. tolypothricoides</i> Kütz.	K, M, H	3, 12, 20
<i>S. varium</i> Kütz.	O	6, 7, 8, 9, 19
<i>Scytonema</i> sp.	O, H	8, 17
<i>Spirulina maior</i> Kütz.	O, H	7, 8, 9, 19
<i>Stigonema mamillosum</i> (Lyngb.) C.Agardh ex Bornet et Flahault	H	12
<i>Tolypothrix distorta</i> (O.F.Müll.) Kütz.	O, H	7, 8, 9, 12, 18, 19
<i>T. nodosa</i> Bharadw.	H	11, 12
<i>T. tenuis</i> Kütz. emend. A.W.F.Schmidt syn. <i>T. lanata</i> (Desv.) Wartmann	O, H	3, 9, 12, 20
<i>Xenococcus kernerii</i> Hansg.	O	6, 7, 8, 9, 19
Chlorophyta		
<i>Basicleadia chelonum</i> (Collins) W.E.Hoffmann et Tilden	O	3, 12, 14
<i>Binuclearia tectorum</i> (Kütz.) S.Berger ex Wichmann syn. <i>B. tatrana</i> Witt.	K	12, 13, 14
<i>Bulbochaete</i> sp.	K, O, H	7, 8, 10, 12, 13
<i>Chaetophora elegans</i> (Roth) C.Agardh	K, O	3, 12
<i>Chaetosphaeridium globosum</i> (Nordst.) Kleb. syn. <i>Herposterion globosum</i> Nordst.	H	6, 9, 10
<i>Chara braunii</i> C.C.Gmelin	O, M	12, 16
<i>C. zeylanica</i> var. <i>diaphana</i> f. <i>armata</i> (F.J.F.Meyen) Zaneveld	K, O	6, 7, 9, 10, 22
<i>Characium groenlandicum</i> Richter	Mo	6, 8, 9
<i>Cladophora fracta</i> (O.F. Müller ex Vahl) Kütz.	O	3, 6, 7, 9, 12

Table 1 (continued)

Taxon	Distribution	References
<i>C. fracta</i> var. <i>rigidula</i> (Kütz.) Rabenh.		21
<i>C. glomerata</i> (L.) Kütz. syn. <i>C. canalicularis</i> (Roth) Kütz.	K, O, M, H	3, 12, 13, 18, 20
<i>C. glomerata</i> var. <i>crassior</i> (C.Agardh) C.Hoek	K, M, H	12, 20
* <i>C. longiarticulata</i> var. <i>valida</i> F.Brand	O	1, 10
<i>C. rivularis</i> (L.) C.Hoek	O	20
<i>C. sericea</i> (Huds.) Kütz. syn. <i>C. nitida</i> Kütz.	O	7, 8, 9
<i>Cladophora</i> sp.	K, O, M	5, 8, 12, 13, 17
<i>Cloniophora macrocladia</i> (Nordst.) Bourr. syn. <i>Draparnaldia macrocladia</i> Nordst., <i>Stigeoclonium macrocladium</i> (Nordst.) Schmidle	K, O, H	4, 6, 7, 8, 9, 10, 12
<i>C. plumosa</i> Kütz. emend. Bory	K, O, M, H	3, 4, 12, 13, 20
<i>C. spicata</i> Schmidle emend. A.K.Islam	K, O, M, H	12, 13, 14
<i>Closteriopsis longissima</i> Lemmerm.	O	6, 7, 8, 9
<i>Coleochaete irregularis</i> Pringsh.	O, H	6, 7, 9, 10
<i>C. orbicularis</i> Pringsh.	O, H	6, 7, 9, 10
<i>Cylindrocystis</i> sp.	H	12
<i>Dactylococcus infusionum</i> var. <i>minor</i> Nordst.	O	6, 7, 9, 10
<i>Desmidium</i> sp.	O, M, H	12
<i>Dictyosphaerium pulchellum</i> H.C.Wood	O	6, 7, 8, 9
<i>Geminella minor</i> (Nägeli) Heering	M, H	12
<i>Haematococcus pluvialis</i> Flot.	throughout	6, 9
<i>Klebsormidium fluitans</i> (Gay) Lokhorst syn. <i>K. rivulare</i> (Kütz.) Morison et Sheath	H	11, 12
<i>K. subtile</i> (Kütz.) Tracanna ex Tell	M	6, 7, 9, 11, 12, 16
<i>Microspora pachyderma</i> (Wille) Lagerh.	K	3, 12
<i>Monoraphidium convolutum</i> var. <i>pseudosabulosum</i> Hindák syn. <i>Dactylococcus infusionum</i> Nägeli		8
<i>Mougeotia capucina</i> (Bory) Nordst.	O, H	6, 7, 9, 10
<i>Mougeotia</i> spp.	K, O, M, H	3, 8, 12, 16
<i>Nitella gracilis</i> ssp. <i>hawaiiensis</i> (Nordst.) R.D.Wood syn. <i>N. hawaiiensis</i> Nordst.	O, H	6, 7, 8, 9, 10, 22
<i>Oedogonium crispum</i> var. <i>hawiense</i> Nordst.	O, H	6, 7, 9, 10
<i>O. globosum</i> Nordst.	O	6, 7, 9, 10
<i>O. undulatum</i> (Bréb.) A.Br.	O	12
<i>Oedogonium</i> spp.	K, O, M, H	3, 5, 7, 8, 12, 13, 17
<i>Pediastrum boryanum</i> (Turpin) Menegh.	H	6, 7
<i>P. duplex</i> var. <i>reticulatum</i> Lagerh. syn. <i>P. duplex</i> var. <i>clathratum</i> A.Braun	O	6, 9
<i>P. integrum</i> var. <i>braunianum</i> (Grunov) Nordst.	H	6, 9, 10
<i>P. tetras</i> (Ehrenb.) Ralfs	O	6, 9, 10
<i>Pediastrum</i> sp.		8
* <i>Pithophora macrospora</i> F.Brand	H	1
<i>Raphidium polymorphum</i> Fresen.	throughout	6, 7, 8, 9
<i>Rhizoclonium crassipellitum</i> W.West et G.S.West	O	11, 12
<i>R. hieroglyphicum</i> (C.Agardh) Kütz.	K, O, M, H	12, 13, 20
<i>R. hieroglyphicum</i> var. <i>hosfordii</i> (Wolle) Collins	K,O	14
<i>Schizomeris leibleinii</i> Kütz.	O, M	12, 14
<i>Schroederia setigera</i> (Schröd.) Lemmerm.	O	6, 7, 8, 9
<i>Spirogyra dictyospora</i> C.C.Jao	M	11, 12, 16
<i>S. dubia</i> Kütz.	M	11, 12
<i>S. elegantissima</i> Ling et Zheng	O, H	11, 12
<i>S. fallax</i> (Hansgirg) Wille	H	11, 12
<i>S. fluviatilis</i> Hilse	H	12, 18

Table 1 (continued)

Taxon	Distribution	References
<i>Spirogyra</i> spp.	throughout	3, 5, 7, 8, 9, 10, 12, 13, 16
<i>Stigeoclonium amoenum</i> var. <i>novizelandicum</i> Nordst.	O	18
<i>S. falklandicum</i> Kütz.	O	6, 7, 9, 10, 18
<i>S. fasciculare</i> Kütz.	K, H	11, 12
<i>S. flagelliferum</i> Kütz.	H	12
<i>S. lubricum</i> (Dillw.) Kütz.	K, O, M	12
<i>S. nudiusculum</i> Kütz.	O	18
<i>S. pachydermum</i> Prescott	K	11, 12
<i>S. segarare</i> A.K.Islam	K	3, 12
<i>S. setigerum</i> Kütz.	O, H	3, 12
<i>S. stagnatile</i> (Hazen) Collins	O, M, H	3, 12, 20
<i>S. subsecundum</i> Kütz.	K, O, H	3, 12, 20
<i>S. tenue</i> (C.Agardh) Kütz.	K, O	7, 9, 20
<i>S. variabile</i> Kütz.	O	12
<i>Stigeoclonium</i> sp.	O	8, 17
<i>Triploceras</i> sp.		8
<i>Ulothrix minutata</i> Kütz.	O	7, 9
<i>U. tenerrima</i> Kütz.	M	12
<i>U. tenuissima</i> Kütz.	H	3, 12
<i>Ulothrix</i> spp.		5, 8
<i>Zygnema</i> spp.	K, O, M, H	8, 10, 12, 13, 20
Rhodophyta		
<i>Audouinella chalybea</i> (Roth) Bory	H	12
<i>A. eugenea</i> (Skuja) C.C.Jao	K, O, M	12, 20
<i>A. pygmaea</i> (Kütz.) Weber Bosse	K, O, H	3, 12, 20
<i>Audouinella</i> sp.	K, O, M	12
* <i>Batrachospermum spermatiophorum</i> Vis et Sheath	M	12, 16, 20
<i>Compsopogon coeruleus</i> (Balb.) Mont.	K, O, M, H	3, 12, 16, 20
syn. <i>Compsopogonopsis leptocladus</i> (Mont.) Krishnamurthy		
<i>Hildenbrandia angolensis</i> Welw. ex W.West et G.S.West	K, O, M, H	3, 12, 13, 20
Dinophyta		
<i>Hemidinium nasutum</i> F.Stein	O	6, 8
Chrysophyta		
<i>Dinobryon sertularia</i> Ehrenb.	Mo	6, 8, 9
Tribophyta		
<i>Tribonema aequale</i> Pascher	H	12
<i>T. affine</i> (G.S.West) G.S.West	O	20
<i>T. elegans</i> Pasch.	K	12
<i>Tribonema</i> sp.	O	12
<i>Vaucheria</i> sp.	O, M	11, 12

flora (19.5%; Abbott, 1999), the angiosperm flora (89%; Wagner & Funk, 1995), and the insect fauna (99%; Wagner & Funk, 1995) of the Hawaiian Islands.

An examination of the number of stream algal records from each broad taxonomic category, by island, indicates that approximately equal proportions of taxa are represented on each island (Fig. 1). This trend is very similar to that previously observed for the stream macroalgal flora, in that the cyanobacteria and Chlorophyta are most strongly represented, followed by the Rhodophyta, with a much smaller proportion represented by the Tribophyta (Fig. 1; Sherwood, 2006).

The “suspiciously cosmopolitan” nature of the Hawaiian stream algal flora

With an estimated 2.3% level of endemism, and a large number of taxa known from a broad range of geographic regions, the Hawaiian stream algal flora is indeed suspiciously cosmopolitan. This is especially true in light of estimates for other groups of the Hawaiian biota (see above section). The cosmopolitan nature of the freshwater algal flora, however, is tightly linked to the species concept employed for the organisms and how it practically relates to species identification. A morphological species concept is most commonly used for freshwater algae (Ichimura, 1996), and, in the vast majority of cases, the taxonomic boundaries are not tested according to the biological species concept (but see McCourt & Hoshaw, 1990 as an example of a rare exception). This can be explained through reasons of practicality – the smallness of size, and either infrequency or outright lack of sexual reproduction for many taxa means that the biological species concept can not be reasonably applied in such studies.

It has been argued that rare taxa may potentially be mistaken for endemics, for example, if insufficient information is available regarding their general distribution (Tyler, 1996). However, given that only four out of 174 taxa in the Hawaiian stream algal flora are believed to be endemic, this is likely not heavily biasing the estimate of endemism for Hawaiian stream algae, at least in a positive direction.

Quickly evolving lineages (relative to dispersal rates) are likely to be characterized by a high degree of endemism (Hoffmann, 1996). Conversely, truly cosmopolitan taxa can only arise if their rate of speciation is slower than their dispersal rate (Hoffmann, 1996). A case could be made for a cosmopolitan freshwater algal flora, based on the information available regarding their dispersal abilities. In general, freshwater algae are believed to take advantage of a number of dispersal means, including water (e.g., within a watershed), other organisms (vectors such as waterfowl and other birds, insects, and mammals, including humans), or air transport (long-distance dispersal by wind) (Kristiansen, 1996). If freshwater algae, or their propagules and reproductive products, are indeed employing all of the above mechanisms for dispersal on a frequent basis, then it is possible that little opportunity exists for reproductive isolation and subsequent speciation. However, one of the hallmarks of the Hawaiian Archipelago is the extreme geographical isolation of the island chain (Juvik & Juvik, 1998). Although freshwater algae may have a remarkably high dispersal capability, the fact remains that Hawai'i is located more than 3,500 km from the nearest continental landmass, and thus it represents a low-probability destination via the above-described dispersal mechanisms. It is almost inevitable, then, that Hawaiian stream algae are on unique evolutionary trajectories, and the signposts of these trajectories may be most easily revealed using molecular techniques. These evolutionary diversions will be interesting to explore since they may give clues as to how the selective pressures operating on Hawaiian stream algae differ from those acting on algae in other geographical locales.

Insights from molecular data – case studies from the literature

In general, researchers do not test their working definitions of taxa through direct application of the biological species concept. However, a number of published studies have examined the molecular diversity patterns for individual taxa of freshwater algae. Such patterns can aid in the discrimination between taxonomic lineages that are truly widespread in geographical distribution, and those that contain previously unsuspected molecular diversity. Some examples are presented below.

The only known study to date to employ molecular markers for taxonomic investigations of Hawaiian stream algae used DNA sequence analysis of the *rbcL* gene (coding for the large subunit

of the Rubisco enzyme) to confirm the endemism of the freshwater red alga, *Batrachospermum spermatiophorum* Vis et Sheath (Sherwood *et al.*, 2004). This distinctive alga was first described and recognized as endemic to the Hawaiian Islands on the basis of its unique morphology and reproductive anatomy (Vis *et al.*, 1994). In this instance, comparisons of *rbcL* gene sequence data from a Hawaiian representative to other sequences of the well-studied and globally distributed genus *Batrachospermum* (e.g., Vis *et al.*, 1998; Vis & Entwisle, 2000) revealed yet another line of evidence to support the endemic status of this alga.

One of the most convincing cases for the inclusion of molecular genetic assessments of individual taxa stems from a study of a freshwater cyanobacterium. The molecular diversity of the cosmopolitan freshwater alga, *Phormidium retzii* (C.Ag.) Gomont, was recently examined by using random amplified polymorphic DNA (RAPD) markers and DNA sequence analysis of the 16S rDNA gene (Casamatta *et al.*, 2003). On the basis of morphological characteristics, this species is one of the most broadly delimited within the cyanobacteria, and it is also widespread throughout Hawaiian stream systems. The levels of genetic diversity found in *P. retzii* samples from throughout the North American range of the taxon were, in some cases, very high for a single species. For example, sequence similarities for the 16S rRNA sequence data comparisons ranged from 88.4–98.4% (Casamatta *et al.*, 2003). Other studies have reported that 16S rRNA sequence similarities of less than 97% are indicative of comparisons between different species (Stackebrandt & Goebel, 1994) and show that the current circumscription of *P. retzii* likely includes a number of different taxa.

As in the previous cyanobacterial case study, some eukaryotic stream algae have also been demonstrated to possess high molecular diversity that is masked by an inconspicuous morphology. For example, the freshwater red alga, *Hildenbrandia angolensis*, was examined as part of a global survey of the order Hildenbrandiales (Sherwood & Sheath, 2003). *Hildenbrandia angolensis* is common in Hawaiian stream systems on all four main Hawaiian Islands, but is commonly overlooked due to its diminutive, crustose morphology (Sherwood, 2006). Comparisons of both the *rbcL* and 18S rRNA genes for samples throughout its range in North America, as well as a single sample from the Philippines, revealed a large amount of genetic diversity within this taxon, compared with other red algae (Sherwood & Sheath, 2003). However, since the pattern of genetic diversity could not be tied to morphological or anatomical characters, taxonomic changes were not effected. Continued study of other characters of this alga, however, such as life history variations, biochemical features, or fine structure, may yield useful taxonomic features that can be used to further discriminate taxa along lines of molecular variation.

Several members of the volvocacean green algae have also been subjects of biogeographic molecular diversity studies. For example, internal transcribed spacer (ITS) DNA comparisons of isolates from widespread collections of *Gonium pectorale* Mueller indicate that only 7% of the DNA sequence positions were variable - an extremely low value (Coleman *et al.*, 1994; Coleman, 1996). Additionally, no cline was found to significantly correlate with the geographic origin of the samples. Thus, *G. pectorale* may indeed be a cosmopolitan taxon. By comparison, the authors used the same technique to examine 12 worldwide isolates of *Pandorina morum* Bory belonging to one of two morphologically indistinguishable “subspecies” or “syngens”, based on interbreeding capabilities (Coleman, 1996). In this case the ITS sequence data suggested that far more DNA sequence diversity was present in *P. morum* than *G. pectorale*, and that syngens are good taxonomic groupings insofar as mating types are more strongly associated than close geographical isolates (Coleman, 1996). Even within the concept of a species, then, it is possible to have morphologically indistinguishable, reproductively isolated lineages with different biogeographic distributions.

Conclusions and Recommendations for Future Research Directions

Based on current understanding of the Hawaiian stream algal flora, most taxa are cosmopolitan in distribution, and very few are endemic to the Hawaiian Islands. However, a true estimate of the endemism of this flora will not be available until molecular methods are employed on a routine basis to confirm or refute the endemic or cosmopolitan nature of the collections. For many studies, however, such as

general ecological investigations, a fine taxonomic scale may not be necessary for the kinds of conclusions being drawn. In any study of stream algae, the taxonomic structure used for identification should be noted so that investigators will be aware of the taxonomic limitations of that study.

Molecular techniques for stream algal systematics research have thus far been largely based on comparative DNA sequence analysis. For conspicuous and character-rich taxa, such as the red alga *Batrachospermum spermatiophorum*, such analyses may not be as critical to include, but, for those “less-charismatic” taxa that comprise the majority of the flora; these methods may uncover revealing patterns of genetic diversity. These patterns may correspond to morphological characters provided sufficient time and effort is spent searching for these connections, for example, at the electron microscopic level. In any case, increased use of molecular data in stream algal taxonomic studies will aid our understanding of the breadth of geographic distribution and the evolutionary diversification of these organisms.

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