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Diversity of the rheophytic condition in bryophytes: field observations from multiple continents

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Abstract

Bryophytes occurring in riparian systems where they are seasonally submerged or inundated are poorly documented in many parts of the world. The actual number of rheophytic bryophytes remains speculative but we believe the number could easily exceed 500 taxa. Rheophytic bryophytes generally display highly disjunct populations and adjacent rivers and streams can have considerably different species composition. Water management in the form of flood control, dams, and hydroelectric development can adversely impact many rheophytic bryophyte species and communities due to changes in river ecology, timing of water flow, and water temperature. Specimens of rheophytic bryophytes are underrepresented in herbaria and labels rarely indicate the actual micro-habitat and ecological attributes for bryophytes collected within riparian systems. Many rheophytes are morphological anomalies compared to their terrestrial relatives and the evolution of the rheophytic condition has occurred repeatedly in many bryophyte lineages.

Key words: aquatic habitats, facultative rheophytes, riparian bryophytes

Introduction

Among the biomes of the world (Box & Fujiwara 2005), species occurring in riparian areas at the interface of water and land appear to be highly restricted and specialized. The term ‘rheophytic’ within an ecological context was advanced in great detail by van Stennis (1981, 1987) whose focus was on vascular plants occurring within the water column of riparian habitats where the plants are influenced by inundation to seasonal submersion. He defined rheophytic plants as “species which are in nature confined to the beds of swift-running water and rivers and grow there up to the flood level, but not beyond the reach of regularly occurring flash floods.” As a habitat type available for colonization, riparian systems are by their nature highly disturbed systems. The fluctuating variability of disturbances is likely to be one of the primary factors influencing rheophyte colonization (Figs. 1–5). While bryophytes can enter riparian areas within streams and rivers as spores, gemmae or even plant fragments, we speculate that it is the establishment phase that is problematic. Any reproductive parts would need to grow and become affixed to the substrate before the next major hydrologic event. Rapid flowing water would tend to wash away any propagules that had not yet given sufficient time to become attached to a substrate, and be able to withstand the first submersion event. Another factor affecting bryophyte growth and maintenance of populations relates to drag coefficients (Glime *et al*. 1979, Suren *et al.* 2000) and the morphological design of various rheophyte mats can provide resistance during peak flows. It also appears that the first successful colonizers in an area become the dominant species through time occupying the best habitats. However, some common rheophytes may be determined by survival rates and those species with a mat-forming growth form are likely to colonize larger surfaces of available habitat. In conducting rheophytic bryophyte surveys in many countries, one of the interesting observations is how different the assemblage of rheophytes can be between adjacent streams and rivers when influenced by the same elevation, geology, vegetation cover, and climate. The observed differences generally can be explained by changes in stream morphology (Rosgen 1994). It may also be a result from the stochastic process when propagules first establish in these highly unstable habitats. In some cases what appears to

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be high quality habitat, rheophytes are either few in number or lacking entirely. These reaches of rivers and streams appear as if unoccupied, yet visually the key attributes are present that could sustain rheophytic bryophyte populations, while in other nearby streams and rivers, boulders in the riparian channel are covered by bryophytes (Suren 1996, Suren & Ormerod 1998, Vieira *et al*. 2016a, b).

Major differences between rheophytic vascular plants and bryophytes

The concept of being rheophytic was articulated by van Stennis (1981, 1987). He divided vascular rheophytes into several categories as hydrophilic, torrenticolous, and the largest group as rheophytic land plants occurring in riparian areas influenced by peak flows. Although van Stennis did not address bryophytes, for the most part, we view these categories are also applicable for bryophytes as well. Van Stennis determined that few vascular plant families were primarily rheophytic. He concluded that certain vascular plant families were more likely to contain rheophytic members based on general design of leaves and propagules, either with evolutionary monospecific genera or members of large genera having rheophytic representatives. We find this condition similar for bryophytes too. For vascular plants with roots, there is a much greater suite of riparian areas available for colonization including flood plains, sandbars, pebble and gravel beds, whereas for bryophytes, substrate stability is considerably more important for species establishment and colonization. In fact, rheophytic bryophytes restricted to the water column of rivers and streams are primarily saxicolous taxa. Species attached to woody substrates such as coarse woody debris (logs), on base of riparian tree trunks, on branches and stems of shrubs hanging over the water surface, or on exposed roots are less common. However, rheophytic bryophytes in the tropics are more frequently encountered on non-saxicolous substrates, especially on shrubs that are inundated or submerged multiple times throughout the year. Although rocky riparian habitats appear ecologically similar from continent to continent, there are few widespread or common rheophytic bryophytes occurring over large geographic areas. In the northern hemisphere, *Fontinalis antipyretica* Hedw. (1801:298–299) may be the most geographically wide-ranging rheophyte.

In his worldwide assessment, van Stennis (1981) determined that rheophytic vascular plants were concentrated in the tropics (especially in Asia based, in part, on his field expeditions) and since the diversity of vascular plants is richest in the tropics, he concluded that rheophytic members should also be similarly concentrated by utilizing this habitat type. However, while bryophyte richness is also expressed with high species diversity in the tropics, a different pattern is emerging for rheophytic bryophytes. Based on our assessment and field work, there appear to be more rheophytic bryophytes in temperate ecosystems than in the tropics, and for Mediterranean climate areas, the number of rheophytes may well exceed 5 percent of the total bryoflora (Table 1). There are also slight differences between mosses and the liverworts for adaptation to rheophytic conditions. Thickened leaf margins and bistratosity of the lamina is considerably more common among rheophytic mosses while this morphological feature is not observed in leafy liverworts. Mosses are generally more capable of withstanding various levels of desiccation, while liverworts usually require longer periods of hydration. Therefore, we encounter more liverworts in the hydrophytic and torrenticolous regions of streams and rivers whereas mosses tend to dominate zones toward the high water mark where they may be exposed for longer periods in a desiccated state. In this paper, we focus on the diversity of rheophytic mosses because we have encountered them more frequently during our field work; clearly the information on rheophytic liverworts is no less important, but currently that information is not as readily available or the number of rheophytic liverworts encountered are considerably fewer in various studies as compared to the mosses (Glime & Vitt 1987, Muotka & Virtanen 1995, Papp 1998, Vanderpoorten & Klein 1999, Heino & Virtanen 2006, Papp *et al*;. 2006, Scarlett & O'Hare 2006). Selected liverwort genera with several rheophytic members that we have collected and observed in the field include: *Chiloscyphus* Corda (1829:651), *Jungermannia* Linnaeus (1753:1131), *Pellia* Raddi (1818: 38), *Plagiochila* (Dumort.) Dumort. (1835:14), *Riccardia* Gray (1821:679), *Scapania* (Dumort.) Dumort. (1835:14) and *Solenostoma* Mitt. (1864:51) to name but a few. In addition, there are rheophytic hornworts such as members of *Folioceros* D.C. Bhardwaj (1971:9) and *Megaceros* Campb. (1907:484). Based on our field experience on multiple continents, we are of the opinion that a greater concentration of rheophytic liverworts will occur in more temperate latitudes or located in mountainous alpine and subalpine areas compared to tropical regions.

Factors and attributes influencing the condition and location of rheophytic habitats

There are many factors and attributes that define the diversity of watersheds expressed as riparian areas. To compare riparian areas across continents, hydrologists have developed a channel classification system as a descriptive way to stratify riparian areas regardless of geography (Buffington & Montgomery 2013). This classification system is

FIGURE 1. A–F. A. Taiwan. Taroko Gorge. Liwa River (lower section) lacking rheophytic bryophytes. The width to depth ratio is too great for the establishment and maintenance of rheophytic bryophytes. Large amounts of silt and sand are deposited during flood events creating non-suitable habitat. B. Yunnan. Gaoligongshan, Pula River. Large granitic boulders in river with rheophytes primarily on the downslope side. C. Guizhou. Maolan National Nature Reserve. Marble rocks covered in *Yunnanobryon rhyacophilum* in cascades and rapids. D. Yunnan. Lijiang. *Sciaromiopsis sinensis* with developing young leaves under fast-flowing water. E. Yunnan. Gaoligongshan. Cascading stream with splash zone carpeted in bryophytes. F. Yunnan. Gaoligongshan. Headwaters of the Pula River, granitic boulders in alpine zone in clean and very cold water covered in *Andreaea, Brachythecium*, and *Bryum*.

described as a hierarchy of Stream Order with Order 1 being confined to headwaters of watersheds where flows are primarily intermittent to Order 12 representing the largest rivers in the world. This system characterizes sections of the watershed and as streams increase in size and complexity they also increase in Order rank. While the Stream Order system based on size is easy to visualize, a classification system focused on the morphological arrangement of actual stream characteristics provides for a more accurate methodology to describe the distribution and colonization of bryophytes along a streambed (Rosgen 1994). The differences between adjacent riparian areas can indeed be significant based on stream attributes such as channel width and depth, stability of the channel, water velocity, slope, disturbance, streamside vegetative cover, and especially for bryophytes, the size and amount of rock within the riparian corridor (Muotka & Virtanen 1995, Vieira *et al*. 2012). It is nonetheless important that stream topologies are likely to have different assessments among taxonomic groups, for example, fish or micro-invertebrates (Paavola *et al*. 2003) as compared to bryophytes. Headwater streams are generally with a steep elevational gradient that creates more rapids, cascades, and waterfalls. Large rivers on the other hand can carry significant amounts of sediment and other materials in the water column making the river milky or muddy in appearance. Besides the size of streams, the geology of the watershed can influence the pH, rates of soil erosion and the type and amount of surrounding terrestrial vegetation. Rheophytic bryophytes can occur in all stream sizes but species composition is also greatly influenced by topography and elevation. Bryophytes occurring in smaller streams and rivers are generally in fast-flowing and cold water where suspended sediments are infrequent and usually present only during peak flow events, and therefore, the water is clear and clean appearing. Large rivers tend to have less rheophyte potential primarily due to less available rock lining the river banks, reduced forest cover, agriculture and other human activities, coupled with significantly greater sediment loads.

The rheophytic condition, therefore, requires several morphological and physiological adaptations in bryophytes (Glime & Vitt 1984a, b, Akiyama 1992b, 1995, Glime 2011). Rheophytes must: 1) tolerate being inundated or submerged for extended periods of time, 2) withstand periods of high velocity water movement, 3) quickly colonize habitat when it becomes available, and 4) withstand various levels of desiccation when the water column is reduced in volume (Shevock *et al.* 2014a). Rheophytic bryophytes occupy a narrow, linear, highly restricted and discontinuous distribution pattern due to the available substratum within the riparian corridor. Most rheophytes are exclusively restricted within the water column of riparian habitats. However, some rheophytes may on occasion expand just beyond the rheophytic zone or a species that is primarily viewed as being terrestrial may in part of its range venture into and occupy rheophytic environments. A good example of the first condition is *Echinodiopsis hispida* (Hook. f. & Wilson) S. Olsson, Enroth & D. Quandt (2011:47) where it is frequently either submerged or in white water rapids in streams and rivers in Tasmania and New Zealand but it can also be found on rocks above streams in high rainfall areas. On the other end of the spectrum is the cosmopolitan moss *Bryum argenteum* Hedw. (1801:181–182) where it can in certain areas be seasonally submerged. Species that can occur within rheophytic habitats but are not restricted to it are called 'facultative rheophytes'. Some genera have species pairs that are clearly related, one being rheophytic and the other terrestrial.

Many rheophytic mosses can be challenging to identify since sporophytes are rarely produced (dioicous taxa) or the conditions required for successful reproduction are limiting; therefore, sporophytes are rarely encountered (Shevock *et al*. 2006, 2011, Ochyra & Shevock 2012, Ma *et al*. 2016b). Often there is a convergence of morphological attributes such as elongate to julaceous shoots, thickened leaf margins and costae, and various degrees of bistratosity across the leaf surface; this creates a suite of taxa that can appear morphologically similar yet phylogenetically not closely related. Many rheophytic liverworts are also similarly challenging to name to species. Why there are so many dioicous rheophytic bryophytes remains a mystery. In such highly altered environments one would suspect that bryophytes would attempt to optimize reproduction as a major function of colonization of habitats and population maintenance. Being dioicous, both sexes would need to arrive, become established, synchronize production of gametangia, and be in close proximity to initiate successful reproduction while in an aquatic environment. However, it appears that vegetative means by plant fragments cast adrift is the most likely pathway used by the majority of rheophytic bryophytes.

Timing, intensity, and frequency of submersion (and the level of desiccation tolerance)

There are three attributes that heavily influence riparian areas as possible habitat zones for the colonization and maintenance of rheophytic bryophyte populations. These attributes center on the amount of water that is discharged through the stream channel. These influential attributes are characterized as the interactions between the **timing**, **intensity**, and **frequency** of submersion. How long a bryophyte will be submerged or desiccated and the intervals (frequency) between these physiological states determines which taxa will find that particular riparian habitat viable for colonization and population maintenance (Glime & Vitt 1984a, b). Therefore, the climate and the seasonal variation of average precipitation are important components influencing which bryophytes can be rheophytic at a particular location. Ecological and micro-habitat attributes will also greatly determine how widespread or restricted a rheophytic moss will be in any watershed (Fritz *et al*. 2009).

FIGURE 2. A–E. A. Yunnan. Gaoligongshan. Headwaters of Zhaobitan River in a mixed conifer-hardwood forest with *Rhododendron*. Boulders covered in rheophytes. B. Doi Inthanon, North Thailand. Small streams are habitat for *Curvicladium kurzii* and *Dixonia orientalis* within evergreen upper montane forests. C. Kaua'i, Hawai'i. Kawaikoi Stream densely covered in *Limbella tricostata* within a tropical rain forest. D. Yunnan. Gaoligongshan. Waterfall covered in rheophytic bryophytes and vascular plants are difficult to survey. Note the amount of rock and logs deposited at base of falls. E. Kaua'i, Hawai'i. Wailua River with rheophytic moss communities over volcanic rock of *Donrichardsia bartramii*, *Ectropothecium zollingeri*, *Glossadelphus limnobioides* and *Papillidiopsis aquatica*.

Stream classification attributes (peak flows, stream depth to width ratio, type of exposed bedrock, geology, water flow velocity, stream/river gradient) all influence the rheophytic environment within the water column and define the wide diversity of riparian systems that exist worldwide (Craw 1976, Watson 1980, Slack & Glime 1985, Odland *et al.* 1991, Jonsson 1997, Stream Bryophyte Group 1999, Downes *et al.* 2003, Tessler *et al.* 2014, Ceschin *et al.* 2015). For bryophyte populations to establish and persist, a combination of these channel attributes determines the level of physiological adaptations necessary for colonization. Where streams are very active with intensive peak flows, the size and stability of rocks in the stream channel becomes critical. For bryophytes tightly attached to the surface of rock walls and boulders, this substrate needs to withstand movement during such flood events. For bryophytes attached to shrubs, this substrate needs to be well anchored and with flexible stems to withstand water movement. If the intensity of flooding and peak flows is so intense and occurs fairly frequently over time, then the entire riparian corridor can be highly scoured and unstable. If the riparian corridor also has a high silt load from erosion of surrounding slopes in the watershed by either natural or human caused activities, bryophytes could be significantly impacted, for example they may be sand-blasted off the rocks. Such riparian areas are unlikely to be colonized by rheophytic bryophytes. Where bryophytes have established, especially on boulders and rock walls, the colonies through time can accumulate silt and sand at the base of stems as water flows over them (Suren *et al*. 2000). These increasing amounts of sediments further binds the bryophyte colonies to the substrate thereby providing additional physical support and soil over rock can also slow the rate of desiccation. In some riparian areas, the depth of sand and silt captured over time at the base of bryophyte shoots can exceed 5 cm (e.g., Akiyama 2013, fig. 2).

In addition to the amount of water moving through a riparian corridor, the timing of that water arrival can be critical. In some river systems, the peak flows occur shortly after snowmelt or during the rainy season. In much of the tropics where the average day length and temperature are fairly constant, peak flows can occur several times during the year, especially during the monsoon season. In some tropical riparian systems where stream and river depths fluctuate markedly even on a daily basis, rheophytes also go through short interval periods of being exposed and submerged. However, in temperate regions, rheophytic bryophytes need to adapt to increasing levels of desiccation, and especially in some systems, bryophytes can be exposed on rock surfaces in full sun during the hottest time of the year. In these situations, acrocarpous mosses tend to dominate. The conditions and length of submersion may also affect the production of gametangia, rate of fertilization, and successful capsule maturation.

Of these many environmental attributes, we view the depth to width ratio of the riparian corridor to be one of the most critical factors in providing suitable habitat for bryophyte colonization. For example, if the depth to width ratio is very low, i.e. shallow and very wide, there is not enough opportunity for bryophytes to be submerged for extended periods of time. On the other end of the spectrum, in streams that are narrow and with a deeper water column, one can observe bands of rheophytes as more habitat is exposed as water level drops. Headwaters of rivers tend to have greater elevational gradient, more cascades, rapids, and even waterfalls. All of these features provide for microhabitat sites available for bryophyte colonization, and therefore increased bryophyte cover.

Intermittent versus perennial watercourses

As mentioned above, the timing of water flow through a riparian system defines many of the conditions for rheophyte colonization and establishment. Van Stennis (1981) also noted that even in deserts there are rheophytic vascular members confined to dry stream channels that are infrequently flooded. However, for bryophytes, such arid areas are unlikely to support any rheophytic species. Of the world biomes (Box & Fujiwara 2005), the Mediterranean climate is a challenge for many bryophytes since there is an extended summer drought period that occurs during the hottest time of the year. Of the 25 identified biodiversity hot spots of the world (Myers *et al.* 2000), all five of the floristic provinces influenced by a Mediterranean climate of cool wet winters and dry hot summers not only have remarkable bryofloras (Sim 1926, Scott & Stone 1976, Catcheside 1980, Magill 1981, 1987, Scott 1994, Magill & Van Rooy 1998, Heyn & Herrnstadt 2004, Malcolm *et al*. 2009, Müller 2009) they also contain a wide array of rheophytic bryophytes (Table 1).

Many rheophytes in Mediterranean climate areas are dry and desiccated for prolonged periods. Climate also plays a key role where significant changes in temperature/day length throughout the year (higher latitudes) can occur versus those with little variation in temperature/day length (broad equatorial zone). Mediterranean bryophytes occurring in the mountains below the snow line are influenced by winter rains where they are actively growing, and by summer drought they are dry and dormant (Shevock 2003). Bryophytes in rivulets, streamlets and other smaller streams fed by snowmelt initiate the production of sporophytes during their seasonal submersion. Rheophytes fused to such sheet-rock rivulets or bedrock will have water flowing over them for only a few weeks, then exposed and dry in full sun until the return of winter storms. In Mediterranean climates, acrocarpous mosses generally dominate where submersion occurs primarily during winter storm events or only for a short period during snowmelt. Members of the Bryaceae and Grimmiaceae are common rheophytes in such habitat types where streams are intermittent.

TABLE 1. Rheophytic mosses of Mediterranean floristic regions. Numbers in parentheses are facultative rheophytes

	Northern Hemisphere		Southern Hemisphere		
Genera with rheophytes	California	Mediterranean	Chile	Australia	South Africa
Andreaea	-	1(2)	2	1	2(2)
Anomobryum	(1)	1	-	-	-
Barbula	-	-	-	(1)	-
Blindia	(1)	1	5	1(1)	1
Brachythecium	2	1		-	(1)
Bryum s.l.	3(3)	6(1)	1	1	2(2)
Calyptrochaeta	-	-	-	-	1
Camptochaete	-	-	-	(1)	-
Cinclidotus	-	3	-	-	-
Cladomniopsis	-	-	1	-	-
Cratoneuron	1	1	-	-	-
Cratoneuropsis	-	-	(1)	1	-
Crumia	1	-	-	-	-
Cyptodon	-	-	-	1	-
Cryphaea	-	-	-	1	-
Cyclodictyon	-	-	-	-	1
Dendrocryphaea	-	1	3	1	-
Dichodontium	2	2	-	-	-
Dicranella	-	-	1	-	-
Didymodon	3(1)	1(1)	-	-	(1)
Distichophyllum	-	-	1	(1)	(1)
Drepanocladus	(1)	2	1	(2)	-
Echinodiopsis	-	-	-	(1)	-
Esosphagnum	-	-	1	-	-
Eurhynchium	-	-	1	1	-
Fissidens	5(1)	5(3)	3	3	2(2)
Fontinalis	7	6	-	-	2
Grimmia	2(2)	(1)	-	-	-
Hygroamblystegium	2	2	-	-	1
Hygrohypnum	5	1	-	-	-
Hyophila	-	-	-	(1)	(1)
Hypopterygium	-	-	-	-	(1)
Isothecium	(1)	1	-	-	-
Kindbergia	(1)	-	-	-	-
Leptodictyum	(1)	1	1	(1)	1
Leucoloma	-	-	-	-	(1)
Ochyraea	4	-	-	-	-
Orthotrichum	2(2)	1(3)	-	-	-
Oxyrrhynchium	(1)	1	-	-	-
Philonotis	(3)	(6)	1	(1)	-
Plagiomnium	(2)	2(1)	-	-	-
Platyhypnidium s. lato	2	2	-	1	1
Pohlia	(2)	(2)	1	-	-
Porothamnium	-	-	-	-	(1)
Porotrichum	(1)	-	-	-	(1)
Pseudoleskea	-	-	-	-	1
Pyrrhobryum	-	-	-	-	(1)
Racomitrium s. lato	6(2)	6	1(1)	1	1(1)
Rhabdodontium	-	-	-	1	-
Rhacocarpus	-	-	-	-	(2)
Sanionia	(1)	1	-	-	-
Schistidium	1(4)	1(2)	1	1	1(1)
Sciuro-hypnum	(1)	2	-	-	-

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TABLE 1. (Continued)

Genera with rheophytes	Northern Hemisphere		Southern Hemisphere		
	California	Mediterranean	Chile	Australia	South Africa
Scleropodium	2	(1)	-	-	-
Scorpidium	-	-	1	-	-
Scorpiurium	-	1	-	-	-
Scouleria	3	-	1	-	-
Sematophyllum	-	-		1	2
Splachnobryum	-	-	1	-	-
Symblepharis	-	-	1	-	-
Thamnobryum	(1)	2	-	1	-
Thuidiopsis	-	-		1	-
Touwia	-	-	-	1	-
Tridontium	-	-	-	1	-
Vescicularia	-	-	-	1	-
Vittia	-	-	3	-	1
Wardia	-	-	-	-	1
Warnstorfia	(1)	1	1	(1)	(1)

How are rheophytes distributed among bryophyte lineages?

There are very few moss families where the majority of species can be characterized as rheophytic (Crosby *et al.* 2000) and the Hygrobiellaceae appears to be the only rheophytic dominated liverwort family (Bakalin, pers. comm.). Examples at the moss family level of being exclusively or highly restricted as rheophytic include the Fontinalaceae with three genera *Fontinalis* Hedw. (1801:298–299) 13 species, *Dichelyma* Myrin (1832:274) 5 species, and *Brachelyma* Schimp. *ex* Cardot (1892:131) 1 species; the Cinclidotaceae confined to the genus *Cinclidotus* P. Beauv. (1804:319) 10 species, and the Scouleriaceae with a single genus, *Scouleria* Hook. (1829:30) 6 species (Glime & Vitt 1984a, Carter *et al*. 2014, Shevock & Norris 2014, Ignatova *et al*. 2015). The Amblystegiaceae *s. lato* has many aquatic species occupying fen and bog habitats, but also a wide diversity of rheophytic members such as *Gradsteinia* Ochyra (1990:19) 1 species, *Hygroamblystegium* Loeske (1903:298–299) 3 species, *Hygrohypnum* Lindberg (1872:277) 8 species, *Hypnobartlettia* Ochyra (1985a:3) 1 species, *Koponenia* Ochyra (1985b:479), 1 species, *Limbella* (Müll. Hal.) Broth. (1927:23) 2 species, *Ochyraea* Váňa (1986:14) 8 species, *Platylomella* A.L. Andrews (1950:58) 1 species, *Sciaromiopsis* Broth. (1924:133) 1 species, *Vittia* Ochyra (1987:391) 1 species and *Wardia* Harv. & Hook. *ex* Hook. (1837:183) 1 species. Other moss families with several rheophytic members include the Brachytheciaceae, Hypnaceae and Neckeraceae (Enroth 1999).

A second group of rheophytes is expressed as a smaller subset of species within large genera such as *Bryum* Hedw. (1801:178) *s. lato, Fissidens* Hedw. (1801:152), and *Schistidium* Bruch & Schimp. (1845:93) where the vast majority of species within these genera are viewed as terrestrial, yet many aquatic and rheophytic species have evolved. In fact, these three moss genera have rheophytic species on all continents. *Fissidens*, with nearly 450 currently recognized species, is likely to be the genus with the most rheophytic members worldwide (Pursell & Shevock 2013). Another large genus with many rheophytic members occurring on multiple continents is *Racomitrium* Bridel (1819:78) *s. lato*.

The third group of rheophytes represent primarily monospecific genera and many are endemic to highly restricted locations. Several of these species are viewed as being rare, uncommon, or of conservation concern. These monospecific genera can morphologically look quite different in appearance from terrestrial relatives of their family. Noteworthy examples include *Handeliobryum sikkimense* (Par.) Ochyra (1986:71) and *Hydrocryphaea wardii* Dixon (1931:4) in the Neckeraceae, both Himalayan taxa extending to southwest China (Ochyra 1986, Enroth 1999, Shevock *et al*. 2006, Ochyra & Shevock 2012), and *Yunnanobryon rhyacophilum* Shevock *et al.* (2011:194) the second genus within the Regmatodontaceae, endemic to southwest China within Guizhou and Yunnan provinces. The monospecific genus *Rhabdodontium* Broth. (1906:803), endemic to Tasmania, was long viewed as a member of the Pterobryaceae, however, based on recent molecular data (Dalton, pers. comm.), it is now transferred to the Ptychomniaceae joining *Cladomniopsis* M. Fleish. (1908:658) as another rheophytic genus in this family. We also find it interesting that so many rheophytic genera are in the Neckeraceae (Enroth 1999) and have highly restricted distributions, such as *Baldwiniella kealeensis* (Reich.) E.B. Bartr. (1933:179) endemic to Hawai'i. Other rheophytes, such as members of the Cryphaeaceae, resemble their terrestrial relatives. In this family, the rheophytic members *Cyptodon* (Broth.) Par. & Schimp. *ex* M. Fleisch. (1914:284) 4 species, *Cyptodontopsis* Dixon (1937:64) 1 species, and *Dendrocryphaea* Par. &

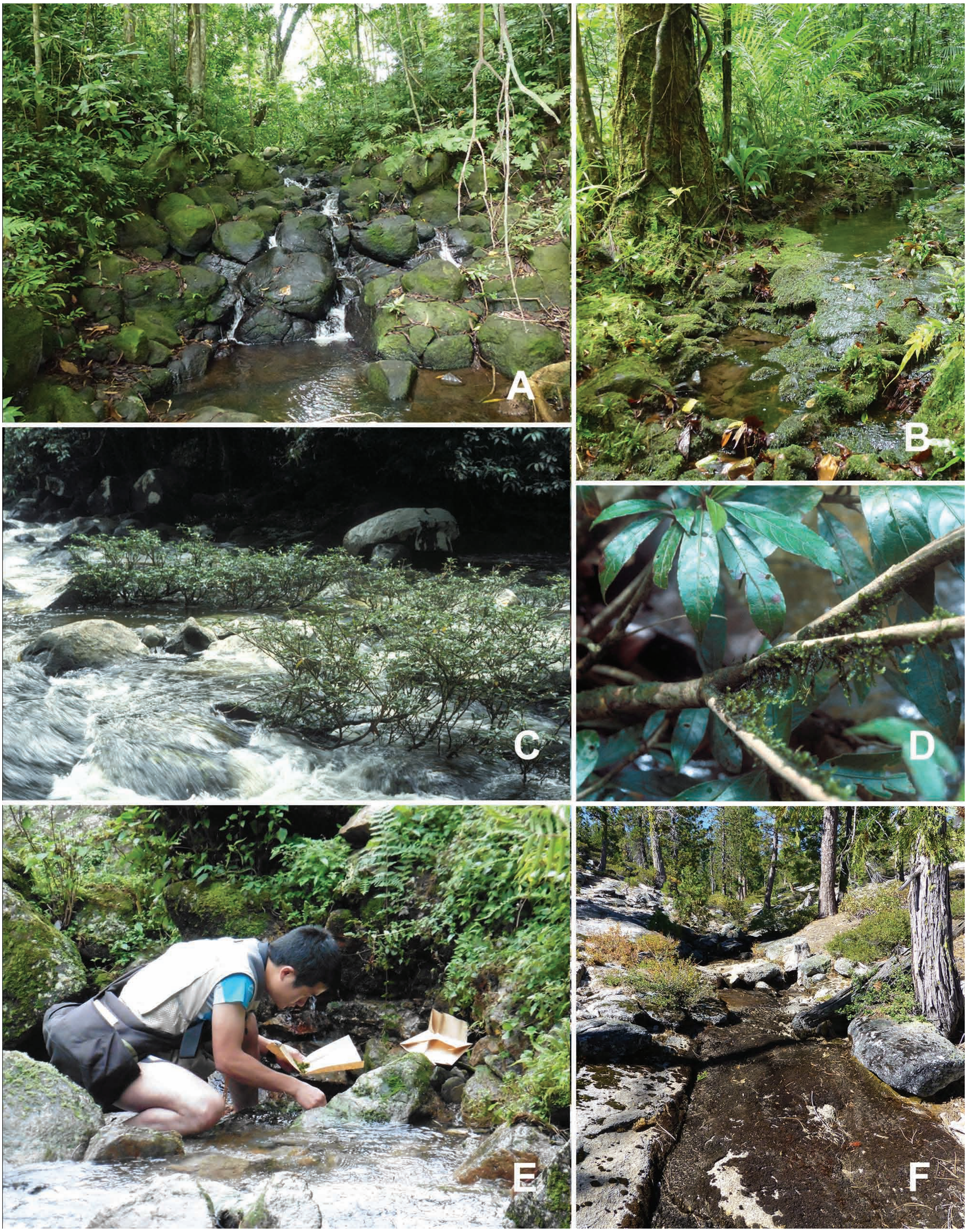

FIGURE 3. A–F. A. São Tomé, west Africa. Small cascading stream over volcanic rock with *Callicostella*, *Fissidens* and *Riccardia* spp. in a lowland tropical rain forest. B. Príncipe, west Africa. Small streamlet flowing after rain events with volcanic bedrock carpeted in bryophytes in a tropical rain forest. C. Dawar, West Kalimantan, Indonesia. Cascading stream with rheophytic shrubs providing habitat for rheophytic bryophytes. D. Dawar, West Kalimantan, Indonesia. *Sclerohypnum littorale* on branches of rheophytic shrub. E. Yunnan. Second author collecting rheophytic mosses in small stream using the packet collecting method. F. California. Sierra Nevada. Mixed conifer forest with intermittent stream channel over granitic bedrock with *Codriophorus acicularis*, *Codriophorus depressus, Grimmia hamulosa, Imbribryum miniatum* and *Schistidium* spp. Plants submerged in fast flowing water during snowmelt then turn dark-colored when desiccated.

Schimp. *ex* Broth. (1905:743) 6 species, produce sporophytes frequently (Enroth 1995, Rao & Enroth 1999, Ma *et al*. 2014).

Rheophytes among tropical regions

Of the major tropical regions within a few degrees of the equator, we know more about rheophytic bryophytes in Asia than we do from Africa or South America. In part, this is the result of a long history and interest of conducting inventory and preparing floristic works in Asia, especially within Malesia (Koponen & Norris 1983, Eddy 1988, 1990, 1996). In Borneo Island (including Kalimantan), a species richness of bryophytes exists at higher elevations (usually above 1000 m asl.). Members of some moss families (i.e. Bartramiaceae, Calymperaceae, Leucobryaceae *s. lato*, Pottiaceae and Sematophyllaceae) can thrive during prolonged dry periods at lower elevations. However, many riparian habitats along river systems also have high levels of suspended sediments visualized as muddy water that can adversely impact bryophytes by depositing large amounts of fine silt, and therefore, such rivers usually contain few rheophytic taxa. Therefore, most rheophytic bryophytes occur at higher elevations, for example, *Neckeropsis beccariana* (Hampe) Touw (1987:103), *Thamnobryum ellipticum* (Bosch & Sande Lac.) Nieuwl. (1917:51) and *Fissidens beccarii* (Hampe) Broth. (1901:362) on boulders; *Calymperes tahitense* (Sull.) Mitt. (1868:172) on hardwood branches or exposed tree roots; and *Sclerohypnum littorale* (Hampe) B.C. Tan (1991:100) on branches of rheophytic shrubs (Akiyama 1992a).

The number of new rheophytic species described from Asia continues to grow (Ochyra & Enroth 1989, Akiyama 1993, 2013, Akiyama & Suleiman 2003, Blom *et al*. 2011, Shevock *et al.* 2011). As more rheophytic habitats are sampled, species new for geographic regions are encountered (Shevock *et. al*. 2006, He & Zhang 2007, Ma *et al*. 2014, 2016a, b). We expect the number of rheophytic bryophytes from both Africa and South America to increase markedly too through future inventory and sampling of riparian habitats (Buck & Hedderson 2016). Shrubs along the river or streambank can be carpeted in bryophytes that are indeed rheophytic, and the same species of shrubs immediately above the high water zone lack rheophytic bryophytes entirely (Ma *et al*. 2014). This linear band of available habitat can be quite narrow. In much of the tropics, these rheophytes are likely to be repeatedly submerged during the year, especially during the monsoon season.

Rheophytes and land species, especially in Asia

Judging from distribution patterns, there are two categories for most rheophytes: they are either widely distributed or narrow endemics. In both cases, we can assume the terrestrial relatives from which rheophyte species might have originated. Representative examples of these relationships are *Diphyscium lorifolium* (Card.) Z.L.K. Magombo (2002:502) versus *D. kashimirense* (H. Rob.) Z.L.K. Magombo (2002:502) (Deguchi 1984, as *Theriotia* Card.), *Hypnodendron milnei* Mitt. (1873:401) ssp. *korthalsii* (Bosch & Sande Lac. *ex* Par.) Touw (1971:302) versus *H. milnei* ssp. *milnei* (Touw 1971), and *Macrothamnium macrocarpum* (Reinw. & Hornsch.) M. Fleisch. (1905:308) versus *M. submacrocarpum* (A. Jaeger *ex* Ren. & Card.) M. Fleisch. (1905:310) (Akiyama 2013, Hayashida *et al.* 2013). Examples of narrow rheophytic endemics with a close terrestrial relative occupying a wider distribution are *Trismegistia maliauensis* H. Akiyama & Suleiman (2003:184) versus *T. lancifolia* (Harv.) Broth. (1908:1078) and *Fissidens dalamair* H. Akiyama (1993:21) versus *F. nobilis* Griff. (1842:505). These examples might be used as case studies for rapid speciation into rheophytic environments.

Rheophytes on islands

Among oceanic islands there are many factors that contribute to the development of a rheophytic bryophyte flora. Size, age, geology, climate and elevation relief, along with distance to nearby land masses, are all important attributes. For example, the tropical island of Kaua'i, (1430 km^2), is distant from other continental land masses, nonetheless, it has a remarkable assemblage of rheophytic members. Among the major Hawaiian island chain, Kaua'i is the oldest island with no active volcanism. Some of its rivers, such as the North Fork Waihua originating from the slopes of Wai'ele'ele, is reported to be among the wettest places on Earth. This river has at least 15 rheophytic mosses, including the Hawaiian endemics *Baldwiniella kealeens*is (Reicht.) E.B. Bartr. (1933:179), *Bryum baldwinii* Broth. (1927:15), *Donrichardsia bartramii* Huttunen & Ignatov (2010:798), *Fissidens pacificus* Ångstr. (1872:21), *Glossadelphus limnobioides* Broth. (1927:32), *Limbella tricostata* (Sull.) Müll. Hal. *ex* E.B. Bartr. (1933:132) and *Rhynchostegium selaginellifolium* Müll. Hal. (1896:475). Remarkably, sporophytes for these species are either unknown or rarely encountered. Other rheophytes in this river system are Asian taxa, with the Hawaiian occurrences representing their easternmost outposts including *Ectropothecium sandwichense* (Hook. & Arn.) Mitt. (1873:400), *E. zollingeri* (Müll. Hal.) A. Jaeg. (1879:272), *Hageniella micans* (Mitt.) B.C. Tan &Y. Jia (1999:37), *Papillidiopsis aquatica* (Dix.) B.-C. Ho & B.C. Tan (2002:74) and *Phyllodon lingulatus* (Card.) W.R. Buck (1987:521). Additional endemic rheophytes restricted to other Hawaiian islands include *Glossadelphus mauiensis* Broth. (1927:31) and *Taxiphyllum torrenticum* (Besch.) W.R. Buck (1987:521).

FIGURE 4. A–E. A. Yunnan. Gaoligongshan. Exposed polished vertical bedrock poses a greater challenge for rheophytic bryophytes to become attached and established. B. Yunnan. Lvshui River, Daweishan National Nature Reserve. *Neckeropsis moutieri* on marble rocks in river. C. California. Rheophytes along Aptos Creek. Vertical walls can only be safely collected during periods of low flow. D. North Island, New Zealand. Tongariro National Park, Waitonga Falls. Cascading stream with *Andreaea*, *Fissidens rigidulus*, *Ochiobryum blandum* and *Rhacocarpus purpuracens* over volcanic boulders in a *Nothofagus* forest. E. São Tomé, west Africa. Small cascading stream over volcanic rock in tropical rain forest with palms. Species in tropical rain forests are basically hydrated for extended periods.

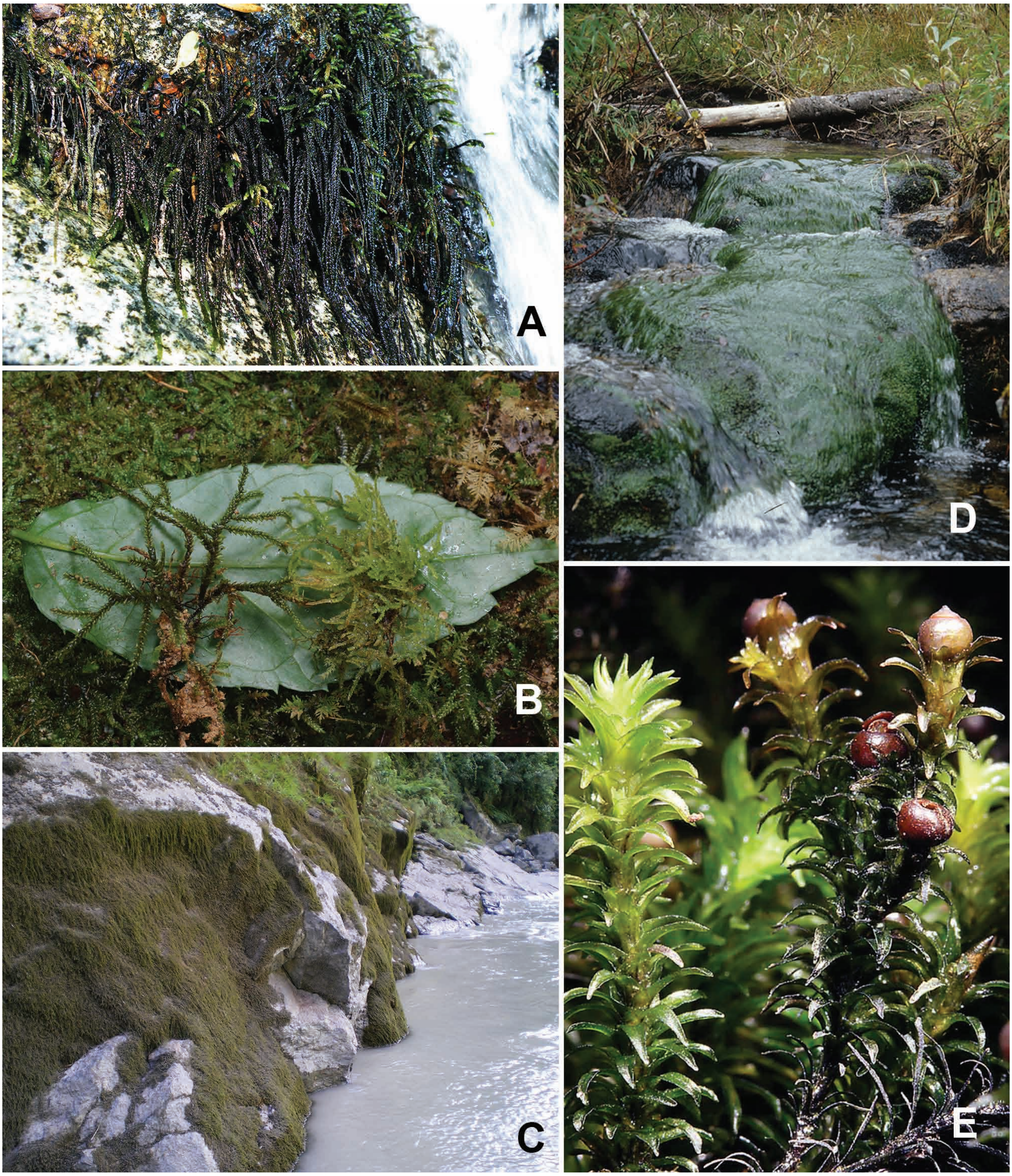

FIGURE 5. A–E. A. Yunnan. Gaoligongshan. *Handeliobryum sikkimense* is restricted to rapids and cascades in fast-flowing streams where rigid stems anchor the plants to the bedrock. B. Doi Inthanon, North Thailand. *Macrothamnium macrocarpum* (a rheophytic species, left) and *M. submacrocarpum* (a terrestrial species, right). The rheophyte is larger, with rigid, longer branches than its terrestrial relative. C. Yunnan. Gaoligongshan. Rock walls below high water mark of the Nu River with *Hydrocryphaea wardii* in mats extending for several meters. The milky coloration of the river is caused by suspended fine silt from melting glaciers. D. Yunnan. Gaoligongshan. Small streamlets in alpine zones can be carpeted of rheophytes such as this dense colony over a meter in size of *Fissidens obscurus*, likely the largest rheophytic member of this genus. E. Oregon. *Scouleria siskiyouensis*.

Other common Hawaiian rheophytes include *Anomobryum angustirete* Broth. (1927:14) and several species of *Philonotis* Brid. (1827:18).

Although we have good documentation of the diversity of Hawaiian rheophytic mosses, other oceanic islands have not received the same level of inquiry. Some well-collected islands such as Réunion in the Indian Ocean, appear to have few documented rheophytes (Hedderson & Ah-Peng pers. comm.). It remains to be determined if there are some ecological reasons why rheophytes are few on this volcanic island. Additionally, recent field work in Samoa by a team from the National Tropical Botanical Garden (PTBG) concluded that rheophytic bryophytes were rare compared to Hawai'i (Flynn, pers. comm.).

Field work by the first author to the tropical oceanic volcanic islands of São Tomé and Príncipe, west Africa has documented several rheophytic bryophytes. Here, species of *Callicostella* (Müll. Hal.) Mitt. (1859:136) and *Porotrichum* (Brid.) Hampe (1863:154) are common rheophytes and many liverworts are also rheophytic, including species of *Jungermannia* Linnaeus (1753:1131), *Plagiochila* (Dumort.) Dumort. (1835:14) and *Riccardia* Gray (1821:679). Along some streams, both *Porotrichum* and *Plagiochila* with a dendoid growth form are intermixed and look nearly identical in size and color and occur in the splash zone of cascades.

Impacts and threats to rheophytic bryophytes

Riparian areas worldwide are under various levels of threat. These impacts come from increasing levels of pollution from cities and agriculture to diversion activities that alter the hydrologic function of riparian systems (Odland *et al*. 1991, Vanderpoorten *et al.* 1999, Downes *et al.* 2003, Vieira *et al.* 2005, 2016a, Papp & Rajczy 2008, Ma *et al.* 2014). Flood control, damming of rivers, and associated hydroelectric development can cause significant changes in the timing, intensity, and frequency of peak flows (Vanderpoorten & Klein 1998, Downes *et al*. 2003, Papp & Rajczy 2008). In some areas, large portions of rivers have become dewatered, channelized, or the timing of the flow has been so altered that rheophytic bryophytes can no longer sustain populations. In many regions with the development of dams and reservoirs, rheophytes have become locally extirpated. Water pollution remains a major concern and rheophytic bryophytes continue to be used in various biomonitoring studies (Vanderpoorten & Palm 1998, Vanderpoorten 1999, Vanderpoorten & Durwael 1999, Yurukova & Gecheva 2004, Gecheva *et al*. 2010, 2011, Ceschin *et al*. 2012).

How many rheophytic bryophytes are there worldwide?

Historically, bryologists have not generally provided detailed ecological data on their specimen labels. Even today, few collectors clearly provide habitat specificity beyond such terms as 'on rock, on tree trunk, on litter' and both locality and ecological data may not even be properly recorded at the time of collection (Shevock *et al.* 2014b). Stating that a collection was made 'along the river' does not provide adequate microhabitat data to determine whether a species is influenced by seasonal submersion and is confined to the water column, and therefore, a rheophytic taxon. Since the number of species in riparian habitats can be limited, this habitat has been less frequently or as intensely sampled compared to adjacent terrestrial environments. Access along many rivers by roads and trails, especially in mountainous and steep terrain, is limited.

Collecting along rapidly flowing rivers and streams can also be dangerous, involving both scrambling about rock walls and boulders, and one generally needs to get in the water column to explore the riparian corridor. Caution should be taken while in narrow canyons and gorges. Rapid change in water levels can occur in very short time spans and the high water (flood zone) can be several meters higher up on the canyon walls compared to low flow periods. Cloud bursts or storms occurring higher up in the watershed can send a torrent of water cascading downslope with little warning or flows altered by discharge from dams and reservoirs upstream. Therefore, field work in such areas requires special attention. These are all factors that have deterred collectors from studying rheophytic bryophytes. The ideal time to collect rheophytes is during the period of the year with minimum water flow exposing more rheophytic habitats and providing safer working conditions to conduct surveys. In tropical areas, the summer monsoon season should be avoided when rivers will be near maximum flow, while in Mediterranean-type climates, the dry summer is usually the best time to sample rheophytes. When specimens are obtained at or below the high water zone, ecological attributes such as being "rheophytic", "seasonally submerged", "inundated", "splash zone", or other descriptive terms, should be recorded on the labels and also indicate if the riparian area is a perennial stream, intermittent or a seasonally flowing streamlet.

We are of the opinion that the number of rheophytic mosses could well exceed 500 species worldwide. Our field experience with rheophytic liverworts is less refined but we predict there will be considerably more liverworts that are rheophytic than the literature or herbarium record would suggest. Even for countries where bryophyte floras or checklists exist, determining which species are rheophytic is a challenge (Shevock *et al.* 2014a). Few checklists identify the preferred habitat and even in published floristic works the habitat for many species is either vague or highly generalized. Some species within floristic treatments that are either poorly known, species not seen in decades, or taxa previously known only from the type specimen, have recently been re-discovered in habitats confirming they are restricted to rheophytic environments (Shevock *et al.* 2006, Ma *et al.* 2014, 2016a). With ongoing field inventory, other rheophytes have been described (Akiyama 1993, Akiyama & Suleiman 2003, Blom *et al.* 2011, Shevock *et. al.* 2011, Shevock & Norris 2014, Buck & Hedderson 2016). Based on our field experience, many more rheophytes are waiting to be documented. Everywhere we have conducted rheophytic surveys, such as in Chile, China, Indonesia, Japan, Philippines, South Korea, Taiwan, tropical west Africa, western North America and even in Hawai'i, we have encountered rheophytes not previously reported. This trend suggests that many more rheophytes will be discovered as bryologists concentrate on sampling this specific habitat type and accurately describe the micro-habitats from which the collections were obtained. Even in landscapes, thought to be well surveyed and have either a checklist or a bryoflora published, new rheophytes await discovery.

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