J. N. Am. Benthol. Soc., 2009, 28(2):397–403

DOI: 10.1899/08–146.1

Are tropical streams really different?

Luz Boyero[1,2,5], Alonso Ramírez[3,6], David Dudgeon[4,7],
AND Richard G. Pearson[1,8]

[1] *School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia*
[2] *Smithsonian Tropical Research Institute, 2072 Balboa-Ancón, Panamá*
[3] *Institute for Tropical Ecosystem Studies, University of Puerto Rico, Río Piedras Campus,*
San Juan, Puerto Rico 00931 USA
[4] *Division of Ecology and Biodiversity, School of Biological Sciences, The University of Hong Kong,*
Hong Kong SAR, China

In the preface of a recent collection of review articles on tropical stream ecology, Dudgeon (2008) stated that there is no such thing as a "typical" tropical stream. The tropics make up the area of the globe between lat 23°N and 23°S, and include a great variety of climatic, geologic, and geomorphologic conditions (Boulton et al. 2008). Thus, tropical streams can flow through landscapes as varied as evergreen rain forests, deciduous seasonal forests, high-altitude grasslands, or even deserts. This diversity suggests that generalizations about tropical streams might be difficult to come by, but it also indicates that much is to be learned about stream ecology in tropical regions.

Several major obstacles hinder the study of tropical streams. An obvious gap is our limited knowledge of their benthic faunas. European, North American, and, to a lesser extent, Australian and New Zealand stream invertebrates have been studied extensively and are well known, but this is not the case for most tropical stream invertebrates. Many insect larval stages have not been related to adults, and identification to species is not possible. Their life histories are unknown, but are often assumed (without good reason) to be similar to those of related temperate taxa. For example, certain traits, such as feeding habits, can differ among close relatives at different latitudes. Baetids and leptophlebiids (Ephemeroptera) are generally scrapers or collector-gatherers in temperate streams, but the baetids, *Acanthiops* from Kenya and *Andesiops* from Bolivia, and the leptophlebiids, *Atalophlebia* from the Australian Wet Tropics and *Barba* from Papua New Guinea, are shredders (Yule 1996, Dobson et al. 2002, Molina 2004, Cheshire et al. 2005).

Studies of tropical streams have been restricted to intense activity by a small number of research groups in a few geographic regions, particularly in Costa Rica, Hong Kong, Kenya, Puerto Rico, Queensland, and Venezuela, although some important work has been done elsewhere. This geographic limitation constrains our ability to understand tropical regions in general. Moreover, it highlights the need for effective communication among dispersed groups of tropical researchers and between workers in tropical and temperate latitudes. Publication of compendia on tropical stream ecology, an activity that the *Journal of the North American Benthological Society* (*J-NABS*) has pioneered, is a powerful tool for enhancing communication and stimulating research in the tropics.

The 1st *J-NABS* special issue on tropical streams was published 20 y ago. It focused on unifying approaches to the study of streams in different biomes (Stanford and Covich 1988) and included topics such as spatial and temporal scales of patchiness and disturbance. The papers in the series mainly reviewed available data from the tropics and emphasized the need for a global perspective when constructing theories for the organization of stream ecosystems (Minshall 1988).

The 2nd *J-NABS* special issue on tropical streams was published in 1995 (Jackson and Sweeney 1995). It focused on descriptive research and included papers on invertebrate taxonomy and life histories, nutrient dynamics, pesticides, and gene flow in invertebrate populations. Only 2 papers, one on leaf-litter processing rates (Campbell and Fuchshuber 1995) and one on disturbance and recolonization of stony substrata (Rosser and Pearson 1995), focused on ecological processes. The range of topics reflected efforts to arrive at a broader understanding of tropical streams,

---

[5] E-mail addresses: luz.boyero@jcu.edu.au
[6] alonso_ites@yahoo.com
[7] ddudgeon@hkucc.hku.hk
[8] richard.pearson@jcu.edu.au

but highlighted the limited amount of information that was applicable at the ecosystem level.

The 3rd *J-NABS* special issue on tropical streams was "New vistas in Neotropical stream ecology" and was published in 2006 (Wantzen et al. 2006). It included studies undertaken at sites in Central and South America and the Caribbean, and embraced an array of topics, including caddisfly biology, organic-matter processing, algal biomass, invertebrate distribution, fish biogeography, and ecological assessment. This issue was concerned solely with the Neotropics, but it demonstrated that understanding of tropical stream ecology had progressed substantially.

This 4th compendium of tropical stream studies arose from a special session, "Are tropical streams ecologically different?," during the 54th annual meeting of the North American Benthological Society (2006; Anchorage, Alaska, USA). The goals of the session were to present novel patterns and notions on the functioning of tropical streams with a special emphasis on energy sources and pathways fueling the ecosystem and the consumers they support and to provide a broad geographical context that would allow comparisons among different tropical areas. This strategy, it was hoped, would yield some generalizations about tropical stream ecosystem processes.

This special issue includes most of the research presented at that session and some additions. Studies represent a wide array of tropical streams, including those in Central America (Costa Rica), South America (Venezuela), Asia (Hong Kong and Peninsular Malaysia), Africa (Madagascar), and the Pacific islands (Micronesia), and some subtropical streams (northern New South Wales, Australia). It includes an analysis of global-scale latitudinal patterns in freshwater biodiversity. Given the small number of studies making up this issue, the extent to which they reveal novel and unexpected patterns is surprising. They confirm the variability of conditions and environments in streams within the tropics and underscore the need for further studies of streams from all tropical regions. Such investigations should include basic taxonomic work, autecological studies, and elucidation of ecological processes and interactions, including foodweb structure and dynamics.

Autochthonous- and Allochthonous-Based Ecosystems

Low-order streams are widely viewed as ecosystems fueled by inputs of detritus from riparian vegetation that enter stream food webs via invertebrate shredders and microorganisms. This model fits most north-temperate forest streams, which support a diverse and abundant shredder fauna, composed mainly of insects (stoneflies and cased caddisflies) and amphipods (Wallace et al. 1997). In tropical streams, a reported scarcity of invertebrate shredders has led to the conclusion that fast litter processing is caused by high rates of microbial activity resulting from high water temperatures (e.g., Irons et al. 1994, Ramírez and Pringle 1998, Dudgeon and Wu 1999, Dobson et al. 2002, Li et al. 2008). A widely held view is that this pattern applies to all tropical regions. However, this generalization is not fully supported, even in those regions used for its formulation. Some tropical streams that lack insect shredders host other shredding consumers, including fishes (Rosemond et al. 2001), shrimps and crabs (March et al. 2001, Dobson 2004), and prosobranch snails (Li and Dudgeon 2008a, Yule et al. 2009). In locations where insects are dominant, correct classification of taxa into functional feeding groups (FFGs; sensu Cummins 1973) has been a problem. Many studies assign tropical stream insects to FFGs according to schema developed for the temperate stream fauna. The classification of Merritt and Cummins (1996) for North American FFGs has been used widely in this regard. That this approach can be misleading has been demonstrated for various insect taxa, especially mayflies (Yule 1996, Dobson et al. 2002, Molina 2004, Cheshire et al. 2005). The matter is complicated by the fact that some taxa can shift their major feeding mode in response to changes in riparian shading (e.g., Li and Dudgeon 2008a). For these reasons, no substitute exists for careful analysis of feeding habits of tropical taxa (e.g., Cheshire et al. 2005, Li and Dudgeon 2008a).

In some tropical regions, the relative importance of shredders is greater than previously thought. For example, Cheshire et al. (2005) found an abundant and diverse shredder assemblage in streams of the Australian Wet Tropics, where heterotrophic pathways based on allochthonous litter appeared dominant. Cheshire et al. (2005) demonstrated that some tropical forest streams function in a way similar to that of their temperate equivalents. Similar results are provided by Yule et al. (2009), who reported the higher diversity of shredders in upland Malaysia streams than has been found thus far at any tropical site. On the other hand, several recent tropical studies concur with Irons et al. (1994). For example, Rincón and Santelloco (2009) report that litter breakdown in some Venezuelan streams is mainly the result of fungal activity, and Jacobsen et al. (2008) suggest a general paucity of shredders in mountain streams at the Ecuadorian Páramo.

Autochthonous algal-based resources also can be important in tropical stream food webs (March and

Pringle 2003). Consumers in some shaded forest streams in Hong Kong rely almost entirely on autochthonous resources (Mantel et al. 2004, Lau et al. 2008, 2009a, b, Li and Dudgeon 2008a). These studies highlight the importance of distinguishing between assimilated and consumed food through stable isotopes and gut content analyses to obtain a reliable picture of the stream food web (Mantel et al. 2004, Lau et al. 2009a). Consumer reliance on autochthonous energy sources in streams where allochthonous detritus is abundant seems paradoxical, but the leaves of tropical evergreen trees are often tough and well defended against terrestrial herbivores by phytochemicals (Coley and Barone 1996, but see Ardón et al. 2009) that can make leaves unpalatable or refractory food sources for shredders and other stream consumers.

Leaves are thought to be a more recalcitrant food source for shredding organisms in the tropics than in temperate regions because leaves of tropical trees are much richer in secondary compounds than are leaves from temperate trees. However, Ardón et al. (2009) demonstrated that concentrations of secondary compounds actually are higher in some temperate leaves than in tropical leaves. Their results underline the importance of using standardized analytical techniques to measure leaf chemistry when making cross-site comparisons. Moreover, comparative studies of leaf toughness are needed because shredders have considerable difficulty feeding on and processing the tough, well-defended leaves of many tropical species (e.g., Li and Dudgeon 2008b). Given the sheer diversity of riparian species in tropical streams (Benson and Pearson 1993, Bastian et al. 2007), substantial effort will be needed to understand how toughness, palatability, and temporal changes in these traits affect shredder species.

Even our incomplete knowledge of tropical streams makes clear the fact that these systems are characterized by complex interactions that are unlikely to be captured adequately by simple generalizations. The data suggest that food webs and the trophic base of production can vary substantially among sites and regions, but we have insufficient information to assess whether such variation is systematic (e.g., by region, realm, or stream type) because the data are geographically limited and the systems that have been studied are patchily distributed.

Gradients within the Tropics

Some of the gradients highlighted in this special issue are natural (e.g., latitude and altitude) and others arise from human disturbance (e.g., landuse change). Gradients in shredder abundance and richness occur in both temperate and tropical regions. For example, few shredders are found in temperate New Zealand streams (Thompson and Townsend 2000), or in tropical Micronesian islands (Benstead et al. 2009), Hawaii (Larned 2000), and parts of Indonesia and New Guinea (Dudgeon 1994, 2006). Isolated island streams tend to have low insect diversity and functionally important decapod macroconsumers, but in some Micronesian islands, leaf litter is broken down mainly by microbial and physical processes (Benstead et al. 2009). In contrast, shredder richness and abundance is high in many temperate streams in North America (Webster et al. 1999) and Europe (Dobson et al. 2002) and in various tropical streams in Queensland (Cheshire et al. 2005) and peninsular Malaysia (Yule et al. 2009). Some of the variation in shredder richness and abundance across tropical streams might reflect variation within regions because shredder abundance seems to vary along elevational as well as latitudinal gradients (Yule et al. 2009).

Upland tropical streams might support a rich shredder fauna composed of taxa typical of temperate streams (limnephilid caddisflies and tipulids) as well as those more characteristic of tropical streams (calamoceratid and certain leptocerid caddisflies). All of these taxa are present in Ecuadorian Páramo streams, but they are rather scarce (Jacobsen 2008) presumably because of the low stature or absence of riparian vegetation at such high altitudes (~4000 m above sea level [asl]). Shredders in Malaysian streams differ between the lowlands and the uplands. Lowland shredders include prosobranch snails, crabs, calamoceratids, and semiaquatic cockroaches, whereas upland shredders are mainly insect taxa similar to those of temperate streams (stoneflies, limnephilids, lepidostomatids, and tipulids; Yule et al. 2009). This pattern might be influenced by the characteristics of available leaves. Dipterocarp trees in Malaysian lowlands typically have tough and leathery leaves, whereas vegetation in the uplands usually is composed of deciduous species with relatively palatable leaves, similar to those in North American and European forests. However, in the Australian tropics, upland and lowland forests typically have similar evergreen species of trees whose leaves are processed by similar species at all altitudes (albeit with a lower range than in other tropical regions).

Landuse change from forest to agriculture is a major anthropogenic alteration that can create strong gradients among streams within the tropics. Understanding how tropical stream ecosystems change in response to land use is a major priority for management and conservation. Biodiversity loss is a well-known response of tropical streams to landuse change (Connolly and Pearson 2005, Ramírez et al. 2008). However, the reduction in diatom species richness caused by forest clearing in Madagascar was an unexpected result (Bixby et al. 2009). As landuse change continues unabated in the tropics, the potential loss of biodiversity is outpacing our ability to understand its implications. Stream ecosystem functions, such as nutrient cycling, also are certain to change with land use (e.g., Tripler et al. 2006), but our understanding of this process in tropical streams is rather limited. An assessment of N cycling in tropical streams in Venezuela highlights the importance of anthropogenic sedimentation in increasing denitrification rates in tropical streams (Solomon et al. 2009). Other anthropogenically induced changes to tropical streams include effects of exotic invaders. Exotic riparian plants might have insidious and unexpected effects on stream ecosystems because exotic leaves can be an unsuitable food source for native fauna in temperate (Graça et al. 2002) and in subtropical streams (Davies and Boulton 2009). The strength of the influence of exotic species in tropical systems remains to be seen, but continuing high rates of deforestation and landuse change are likely to provide opportunities for many invasive plants along stream margins.

Are Tropical Streams More or Less Diverse than Temperate Streams?

The debate is long-standing regarding the existence in stream systems of the expected (on the basis of patterns in terrestrial systems) trend of increasing species diversity with decreasing latitude (Boyero 2002). The discussion has focused largely on site-based studies, such as those collated by Vinson and Hawkins (2004; 495 long-term studies). Pearson and Boyero (2009) have taken a different approach by looking at regional faunas (see also Boulton et al. 2008). They show that different major taxa have different patterns of global distribution. Some groups (frogs, fishes, decapod crustaceans, prosobranch snails, odonates) are more diverse in tropical regions, some are more diverse in temperate regions (stoneflies, limnephilid and phryganeid caddisflies), and others do not appear to vary with latitude (mayflies). Pearson and Boyero (2009) also show that the pattern of latitudinal variation can vary substantially within taxa. For example, different families of Caudata (salamanders and newts) have contrasting latitudinal patterns of diversity.

Moreover, the evolutionary setting can affect patterns of diversity. For example, Pearson and Boyero (2009) show that some amphibiotic taxa that are diverse in the tropics have a long terrestrial phase and a relatively short aquatic phase (e.g., odonates), whereas other amphibiotic taxa that are diverse in the temperate zone have a long aquatic phase and a short adult phase (e.g., mayflies) (see also Boulton et al. 2008). Pearson and Boyero (2009) propose explanations for this contrast in different ecological and evolutionary contexts. Currently, inadequate published information exists with which to investigate this pattern in many taxa, and no comparative studies of species assemblages across aquatic and terrestrial habitats that might help explain the patterns appear to have been done. For example, an investigation of the niche dimensions and constraints of odonate assemblages in streams (larvae) and contiguous forest (adults) might be very rewarding.

Conclusions

One reason for compiling this series of papers in a single issue of *J-NABS* was to investigate the energy sources fueling tropical stream ecosystems. Some appear to be based almost completely on autochthonous resources, whereas others rely on allochthonous material. In some of the tropical streams that depend on leaf litter inputs, allochthonous resources were processed via detritivore pathways, in ways similar to those described for temperate streams. In other tropical streams, allochthonous resources were used through a combination of microbial activity, physical action, and sometimes macroconsumers (fishes and shrimps). The existence of gradients and scales of variation within the tropics has been neglected and will have to be better understood before we can explain the apparent inconsistencies in energy flow and other processes among tropical stream ecosystems.

Studies in this special issue reveal that an array of gradients related to climatic conditions, land use, and biogeography influence tropical streams. High-altitude tropical streams might be functionally more similar to temperate streams than to their lowland counterparts. However, they might differ from temperate streams because of the more constant conditions of light and temperature in the tropics than in temperate regions. Lowland tropical streams might differ much more substantially from temperate streams than do high-altitude tropical streams, particularly in terms of faunal composition, trophic structure, and ecosystem functioning. Thus, we must ask how climate change might affect these characteristics. The need is urgent to develop latitudinally and regionally appropriate models that link ecological responses in tropical streams to changes in rainfall and discharge, temperature, riparian vegetation, and the greater frequency of droughts and spates. Without an ability to predict the consequences of such changes, management strategies are unlikely to meet with much success. The consequences of such failure for tropical freshwater biodiversity cannot be predicted with certainty, but could well be grave.

No single schema can accurately describe all tropical streams, but this fact should be expected. We already know it is true of temperate streams. The tropical zone has a wider array of conditions such as temperature, humidity, and plant diversity than does the temperate zone, so it is certain to support a wider range of ecosystems. We need to understand the structure and function of these systems at least as well as we understand those of temperate systems before we can make in-depth comparisons between latitudinal zones. Standardized tools and techniques are needed to enable comparisons of stream ecosystems across latitudinal gradients. This approach has rarely been used, although Lake et al. (1994) were able to compare invertebrate diversity in temperate and tropical Australian streams by using identical methods in very similar streams.

The need for more taxonomic and basic ecological work in tropical streams is clear (Boyero 2000), but decades (the time needed to achieve our present understanding of temperate streams and the few tropical streams that have been studied) probably will pass before that information will be available. Meanwhile, we must not assume that the structure and functioning of tropical systems is identical to that of their temperate counterparts (or that it is alike in all tropical systems). We must eliminate the "temperate intellectual hegemony" of which Dudgeon (2008), quoting the late W. D. Williams, warns. We must keep an open mind if we hope to detect and investigate new patterns that do not fit into current models or thinking.

Literature Cited

ARDÓN, M., C. M. PRINGLE, AND S. L. EGGERT. 2009. Does leaf chemistry differentially affect breakdown in tropical versus temperate streams? Importance of using standardized analytical techniques to measure leaf chemistry. Journal of the North American Benthological Society 28:440–453.

BASTIAN, M., L. BOYERO, B. JACKES, AND R. G. PEARSON. 2007. Leaf preferences by shredders in tropical streams. Journal of Tropical Ecology 23:219–229.

BENSON, L. J., AND R. G. PEARSON. 1993. Litter inputs to a tropical Australian upland rainforest stream. Australian Journal of Ecology 18:377–383.

BENSTEAD, J., J. G. MARCH, C. M. PRINGLE, K. C. EWEL, AND J. W. SHORT. 2009. Biodiversity and ecosystem function in species-poor communities: community structure and leaf litter breakdown in a Pacific island stream. Journal of the North American Benthological Society 28:454–465.

BIXBY, R. J., J. P. BENSTEAD, M. M. DOUGLAS, AND C. M. PRINGLE. 2009. Relationships of stream algal community structure to catchment deforestation in eastern Madagascar. Journal of the North American Benthological Society 28:466–479.

BOULTON, A. J., L. BOYERO, A. P. COVICH, M. DOBSON, P. S. LAKE, AND R. G. PEARSON. 2008. Are tropical streams ecologically different from temperate streams? Pages 257–284 *in* D. Dudgeon (editor). Aquatic ecosystems: tropical stream ecology. Elsevier Science, London, UK.

BOYERO, L. 2000. Towards a global stream ecology. Trends in Ecology and Evolution 15:390–391.

BOYERO, L. 2002. Insect biodiversity in freshwater ecosystems. Is there any latitudinal gradient? Marine and Freshwater Research 53:753–755.

CAMPBELL, I. C., AND L. FUCHSHUBER. 1995. Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. Journal of the North American Benthological Society 14:174–182.

CHESHIRE, K., L. BOYERO, AND R. G. PEARSON. 2005. Food webs in tropical Australian streams: shredders are not scarce. Freshwater Biology 50:748–769.

COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305–335.

CONNOLLY, N. M., AND R. G. PEARSON. 2005. Impacts of forest conversion on the ecology of streams in the humid tropics. Pages 811–830 *in* M. Bonell and L. A. Bruijnzeel (editors). Forests, water, and people in the Humid Tropics. Cambridge University Press, Cambridge, UK.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183–205.

DAVIES, J. N., AND A. J. BOULTON. 2009. Great house, poor food: effects of exotic leaf-litter on shredder densities and caddisfly growth in 6 subtropical Australian streams. Journal of the North American Benthological Society 28: 491–503.

DOBSON, M. 2004. Freshwater crabs in Africa. Freshwater Forum 21:3–26.

DOBSON, M., A. MAGANA, J. M. MATHOOKO, AND F. K. NDEGWA. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? Freshwater Biology 47:909–919.

DUDGEON, D. 1994. The influence of riparian vegetation on macroinvertebrate community structure and functional organization in six New Guinea streams. Hydrobiologia 294:65–85.

DUDGEON, D. 2006. The impacts of human disturbance on stream benthic invertebrates and their drift in North Sulawesi, Indonesia. Freshwater Biology 51:1710–1729.

DUDGEON, D. 2008. Preface. Pages XV–XVII *in* D. Dudgeon (editor). Aquatic ecosystems: tropical stream ecology. Elsevier Science, London, UK.

DUDGEON, D., AND K. K. Y. WU. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? Archiv für Hydrobiologie 146:65–82.

GRAÇA, M. A. S., J. POZO, C. CANHOTO, AND A. ELOSEGI. 2002.

Effects of eucalyptus plantations on detritus, decomposers, and detritivores in streams. TheScientificWorld 2: 1173–1185.

Irons, J. G., M. W. Oswood, R. J. Stout, and C. M. Pringle. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? Freshwater Biology 32: 401–411.

Jackson, J. K., and B. W. Sweeney. 1995. Research in tropical streams and rivers: introduction to a series of papers. Journal of the North American Benthological Society 14: 2–4.

Jacobsen, D. 2008. Tropical high-altitude streams. Pages 219–256 *in* D. Dudgeon (editor). Aquatic ecosystems: tropical stream ecology. Elsevier Science, London, UK.

Jacobsen, D., C. Cressa, and D. Dudgeon. 2008. Macroinvertebrates: compostion, life histories and production. Pages 65–105 *in* D. Dudgeon (editor). Aquatic ecosystems: tropical stream ecology. Elsevier Science, London, UK

Lake, P. S., E. S. G. Schreiber, B. J. Milne, and R. G. Pearson. 1994. Species richness in streams: patterns over time, with stream size and with latitude. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 25:1822–1826.

Larned, S. T. 2000. Dynamics of coarse riparian detritus in a Hawaiian stream ecosystem: a comparison of drought and post-drought conditions. Journal of the North American Benthological Society 19:215–234.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2008. Experimental dietary manipulations for determining the relative importance of allochthonous and autochthonous food resources in tropical streams. Freshwater Biology 53:139–147.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009a. What does stable isotope analysis reveal about food webs and trophic relationships in tropical streams? A synthetic study from Hong Kong. Freshwater Biology 54:127–141.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009b. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28:426–439.

Li, A. O. Y., and D. Dudgeon. 2008a. Food resources of shredders and other benthic macroinvertebrates across a range of shading conditions in tropical Hong Kong streams. Freshwater Biology 53:2011–2025.

Li, A. O. Y., and D. Dudgeon. 2008b. The effects of leaf litter characteristics on feeding and fitness of a tropical stream shredder. Marine and Freshwater Research 59:897–901.

Li, A. O. Y., L. C. Y. Ng, and D. Dudgeon. 2008. Influence of leaf toughness and nitrogen content on litter breakdown and macroinvertebrates in a tropical stream. Aquatic Sciences. doi: 10.1007/s00027-008-8117-y

Mantel, S. K., M. Salas, and D. Dudgeon. 2004. Food web structure in a tropical Asian forest stream. Journal of the North American Benthological Society 23:728–755.

March, J. G., J. P. Benstead, C. M. Pringle, and M. W. Ruebel. 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries and Aquatic Sciences 58:470–478.

March, J. G., and C. M. Pringle. 2003. Food web structure and basal resource utilization along a tropical island stream continuum, Puerto Rico. Biotropica 35:84–93.

Merritt, R. W., and K. W. Cummins (editors). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.

Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. Journal of the North American Benthological Society 7:263–288.

Molina, C. I. A. 2004. Estudios de los rasgos biológicos y ecológicos en poblaciones de los órdenes: Ephemeroptera, Plecoptera y Trichoptera (clase Insecta), en un río al pie del glaciar Mururata. BSc Thesis, Universidad Mayor de San Andres, La Paz, Bolivia.

Pearson, R. G., and L. Boyero. 2009. Gradients in regional diversity of freshwater taxa. Journal of the North American Benthological Society 28:504–514.

Ramírez, A., and C. M. Pringle. 1998. Structure and production of a benthic insect assemblage in a neotropical stream. Journal of North American Benthological Society 17:443–463.

Ramírez, A., C. M. Pringle, and K. M. Wantzen. 2008. Tropical stream conservation. Pages 285–304 *in* D. Dudgeon and C. Cressa (editors). Aquatic ecosystems: tropical stream ecology. Elsevier Science, London, UK.

Rincón, J., and R. Santelloco. 2009. Aquatic fungi associated with decomposing *Ficus* sp. leaf litter in a neotropical stream. Journal of the North American Benthological Society 28:416–425.

Rosemond, A. D., C. M. Pringle, A. Ramírez, and M. J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. Ecology 82:2279–2293.

Rosser, Z., and R. G. Pearson. 1995. Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. Journal of the North American Benthological Society 14:183–196.

Solomon, C. T., E. R. Hotchkiss, J. M. Moslemi, A. J. Ulseth, E. H. Stanley, R. O. Hall, and A. S. Flecker. 2009. Sediment size and nutrients regulate denitrification in a tropical stream. Journal of the North American Benthological Society 28:480–490.

Stanford, J. A., and A. P. Covich. 1988. Preface. Journal of the North American Benthological Society 7:261–262.

Thompson, R. M., and C. R. Townsend. 2000. New Zealand's stream invertebrate communities: an international perspective. Pages 257–284 *in* K. J. Collier and M. J. Winterbourn (editors). New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Society, Christchurch, New Zealand.

Tripler, C. E., S. S. Kaushal, G. E. Likens, and M. T. Walter. 2006. Patterns in potassium dynamics in forest ecosystems. Ecology Letters 9:451–466.

Vinson, M. R., and C. P. Hawkins. 2004. Broad-scale geographical patterns in local stream insect genera richness. Ecography 26:751–767.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster.

1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

WANTZEN, K. M., A. RAMIREZ, AND K. O. WINEMILLER. 2006. New vistas in Neotropical stream ecology—preface. Journal of the North American Benthological Society 25:61–65.

WEBSTER, J. R., E. F. BENFIELD, T. P. EHRMAN, M. A. SCHAEFFER, AND J. L. TANK. J. J. Hutchens , and D. J. D'Angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41:687–705.

YULE, C. M. 1996. Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea. Journal of Tropical Ecology 12:517–534.

YULE, C. M., M. Y. LEONG, K. C. LIEW, L. RATNARAJAH, K. SCHMIDT, H. M. WONG, R. G. PEARSON, AND L. BOYERO. 2009. Shredders in Malaysia: abundance and richness are higher in cool upland tropical streams. Journal of the North American Benthological Society 28:404–415.

Received: 16 October 2008
Accepted: 12 December 2008