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Are Tropical Streams Ecologically Different from Temperate Streams?

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If tropical streams differ ecologically from temperate ones, we must be cautious in our extrapolation of ecosystem models developed in temperate-zone streams. Similarly, approaches and techniques used routinely in management of temperate streams may not be applicable in the tropics. Despite considerable variability in geological history, flow regime and geomorphology, streams in the tropics typically receive higher insolation and more intense rainfall, with warmer water and often relatively predictable floods. For many groups of aquatic taxa, tropical streams also harbour higher biodiversity than their temperate equivalents. Nonetheless, there is little published evidence for consistent differences in food-web structure, productivity, organic-matter processing and nutrient dynamics, or responses to disturbance which would indicate that the term 'tropical' has special significance when applied to stream ecology. Instead, ecological processes in tropical streams appear to be driven by the same variables that are important in temperate ones. For example, biotic responses to drought and flooding are similar to those in temperate streams while in-stream productivity is limited by the same factors: nutrients, shading, disturbance, and trophic structure. Shredders are reputed to be rare in many tropical streams but this also is the case in many southern temperate streams, implying that models of leaf breakdown developed in the north-temperate zone may not have the universal applicability often assumed. Biome comparisons among temperate and tropical streams are confounded by the immense inherent variability of streams within both these zones, and the wide range of climatic and hydrological conditions – even in the tropics. Valid extrapolation of models and management strategies may be less a matter of tropical versus temperate streams but, instead, of ensuring comparability at appropriate scales and fuller understanding of ecological mechanisms, plus recognition of the magnitude and complexity of spatial and temporal variation in stream ecosystems at all latitudes.

I. INTRODUCTION

Are tropical streams ecologically different from temperate streams? Against the backdrop of 'ecology's oldest pattern' (Hawkins, 2001) that diversity in the tropics far exceeds that of temperate zones, posing this question may seem superfluous. However, the observed latitudinal

differences in biodiversity are not consistent across broad taxonomic groups and have multiple explanations (e.g. Rohde, 1992; Rosenzweig, 1997). When present, these patterns of biodiversity may generate significant differences in food-web structure and productivity that are at odds with predictions from models developed in temperate streams (Covich, 1988). Wide variation in climate, geomorphology, landscape evolution, and geological history across tropical zones potentially masks patterns that might be considered 'unique' to tropical streams (Wantzen *et al.*, 2006). It is also likely that the local variation among streams found within tropical and temperate zones is so great that latitudinal trends in regional ecological drivers such as temperature, photoperiod, and seasonality seldom are detectable. Here, we address the following questions: is the perception that tropical streams are very different ecologically from temperate ones based on facts or assumptions? Does such a perception result from inappropriate comparisons confounded by differences in geology, flow regime, disturbance history, sampling procedures and taxonomic resolution, biogeography, anthropogenic influence, and uneven data sets?

We follow the latitudinal definition of 'tropical' used elsewhere in this book (see Chapter 1) to encompass streams lying between 23°N and 23°S but, where appropriate, extend this to include areas where monsoonal seasonal rains fall. While it is futile to attempt to draw firm boundaries across a climatic continuum, for ease of discussion and from widespread precedence in the scientific literature we use the terms 'tropical' and 'temperate' as adjectives for regional comparisons of their stream ecology. Despite the impossibility of drawing generalizations about an idealized 'tropical' or 'temperate' stream, there is a need to compare ecological processes and diversity in equivalent-sized streams from different parts of tropical and temperate regions. This comparison is necessary because the vast amount of research undertaken on north temperate streams has given rise to ecological models (e.g. the River Continuum Concept: Vannote *et al.*, 1980; the Riverine Productivity Model: Thorp and Delong, 1994) that are now being used to guide research questions and management approaches in rivers worldwide. The flood pulse concept (Junk *et al.*, 1989; Junk and Wantzen, 2004), developed in tropical rivers, is a notable exception to this generalization. However, if tropical streams are ecologically different from temperate ones, uncritical extrapolation of these models may be seriously misleading (Covich, 1988; Dudgeon, 1999a; Dudgeon *et al.*, 2000; Pringle *et al.*, 2000a; Bass, 2003; Wantzen *et al.*, 2006).

Systematic differences between the ecology of tropical and temperate streams could also invalidate commonly-used management strategies that have been developed and tested in temperate streams. For example, faecal coliforms are used routinely as indicators of recent faecal contamination in waterways in the United States, Europe and Australia. However, in some tropical streams relatively undisturbed by human activity, Carillo *et al.* (1985) found high counts of faecal coliforms including *Escherichia coli*, apparently promoted by the natural tropical patterns of high water temperatures and humidity. Another example is the failure in many tropical rivers of the common biological index for stream health derived from counts of the sensitive insect orders of Ephemeroptera, Plecoptera and Trichoptera (EPT) because representatives of the Plecoptera are naturally absent or rare (Dudgeon, 1999a; Vinson and Hawkins, 2003).

Many papers describing ecological phenomena from tropical streams compare their results with those from temperate counterparts (Greathouse and Pringle, 2006) but sometimes ideas developed in the tropics are applied to temperate stream ecosystems. For example, Benke *et al.* (2000) applied the flood pulse concept developed for the Amazon basin (Junk *et al.*, 1989) to a smaller north-temperate drainage system in Georgia. In another example, Dobson *et al.* (2002) make the case that apparently low populations of leaf-shredding invertebrates in many tropical streams may demonstrate that the popular model of leaf breakdown with its emphasis on mediation by shredders could actually be an unusual feature, more representative of streams in the north temperate zone and not a global mechanism of detrital processing. Shredders have also been shown to be uncommon in many streams in south-temperate latitudes (e.g. Winterbourn *et al.*, 1981; Lake *et al.*, 1986) and this global pattern deserves further attention so that it can

be elucidated more clearly. Examples of the limited generality of concepts will likely increase as more ecologists explore the similarities and differences among streams across latitudes. Given that tropical catchments cover the largest area of the Earth's climatic zones, we need broader, more representative studies from these potentially different regions (Wantzen *et al.*, 2006).

This chapter explores the evidence for and against the proposition that there are fundamental differences in the ecology of temperate and tropical streams. First, we examine the evidence for qualitative differences in climate, hydrology and geomorphology between tropical and temperate streams that might generate a habitat template for ecological differences. We then compare aspects of their biodiversity and biogeography, food-web organization and trophic structure, primary productivity and organic matter dynamics, and the role of disturbance. We seek to determine whether trends in these variables are merely quantitative variations across latitudes, and whether the term 'tropical' can be ecologically informative when discussing streams and rivers. We also speculate on potentially productive research directions in instances where the search for comparisons has revealed substantial knowledge gaps or generated broad-scale hypotheses that could be tested by inter-biome comparisons.

II. TROPICAL SETTINGS: INTERACTIONS BETWEEN CLIMATE AND LANDSCAPE EVOLUTION

A. Geological History and Geomorphology

Tropical land masses span a broad range of geological history ranging from the relatively young islands of the South Pacific created by tectonic upheaval and volcanism (Craig, 2003) to the ancient Precambrian drainage basins of many tropical continental regions, such as the Niger in Africa (Alagbe, 2002), where effects of sea-level change and plate movement have been minimal. Furthermore, most tropical streams in low-elevation drainage basins are older than those found in the temperate zones of North America and Europe where glaciation created 'lake districts' drained by a network of rivers of similar ages. Their location near the equator, and well away from the polar caps, has meant that some of the Earth's largest rivers (e.g. Amazon, Orinoco, and Mekong) are also among the oldest, with major biogeographical and biodiversity implications. For example, the Amazon and Orinoco have been estimated to support (respectively) 3000 and 2000 fish species (Lowe-McConnell, 1987), although the actual totals may be higher (see also Chapter 5 of this volume). At the other end of the tropical spectrum in age and stream size, the geologically recent and insular streams of the Caribbean and South Pacific have fewer than 10 fish species, and this is typical of tropical oceanic islands (Pringle *et al.*, 2000a; Donaldson and Myers, 2002).

Differences in geological histories have significant implications for the geomorphology of their rivers. Physical controls on stream-channel dynamics include formation of steep waterfalls in areas of tectonically uplifted terrain (Craig, 2003), along with potentially rapid erosion, formation of landslides and extensive deposition of sediments (Ahmand *et al.*, 1993), especially prevalent in young drainage basins. In these types of stream channel, sediments are typically coarse, riffles and glides are common, and pools are relatively shallow. Hydrological responses to heavy rain in these systems are flashy, with scouring spates commonly disturbing the stream biota and mobilizing organic matter and sediments (Covich *et al.*, 1991, 2006; Johnson *et al.*, 1998). The same disturbances occur in equivalent temperate streams on steep mountains (Benda and Dunne, 1997; Woodward and Hildrew, 2002) with similar physical impacts on stream ecosystem properties (e.g. Kiffney *et al.*, 2004).

Older rivers have more weathered catchments and well-developed alluvial lowland plains where floodplain ecosystems are long-established and diverse (Chestnut and McDowell, 2000). The drainage boundaries of many large tropical rivers are physically defined by ridges and

valleys of different geologic ages, yielding different combinations of weathered elements and macronutrients (Markewitz *et al.*, 2001). Not surprisingly, most of the processes of abiotic weathering and leaching match those observed in temperate rivers (e.g. McDowell, 1998), with the main difference that such processes have been occurring for longer in many ancient tropical drainages and, therefore, the sediments would be more weathered (White *et al.*, 1998). However, an important distinction must be made between the weathering processes in the wet-dry tropics versus those in the humid tropics where the differences are more driven by hydrological patterns than historical variables. Osterkamp (2002) claims that features typical of the humid tropics (e.g. frequent and intense storms; intense biochemical weathering; hill slope creep and landslides favoured by a deep, chemically weathered regolith) promote more rapid weathering and subsequent water transport of the products of weathering than in equivalent-aged temperate catchments. Conversely, in the wet-dry tropics, alternation of inundation and desiccation may expedite release of weathered nutrients that are then taken up by geochemical and microbial processes, resulting in the dilute chemical composition of many tropical rivers (Stallard, 2002).

Selective leaching of silica (White *et al.*, 1998), the main constituent of most rocks, degrades mineral structure and leads to silica-poor clays in tropical river basins. Successive cycles of wetting and baking of these clays cause physical stress, swelling and cracking of soils, and increases the mobilization of nutrients (Twinch, 1987). Temperature also plays a major role, through its action on physical disintegration of rocks and thermal enhancement of chemical and biological weathering processes. The ionizing power of water increases steeply with temperature, being four times higher at 25°C than at 10°C so that chemically aggressive solutions can penetrate deep into rock (Faniran and Areola, 1978). Intense storms, typical of the tropics (see below), contribute to the accelerated erosion and transport of weathered sediments. Overall, patterns of weathering and geomorphological processes are likely to be complex derivatives of geological history, rock type, climate, and hydrology – any influence of latitude is probably largely via the effects of the generally higher temperatures. As shown in Chapter 1 of this volume, maximum water temperatures of 25–35°C occur at low to moderate elevations in the tropics, and this would be expected to influence weathering rates as well as oxygen saturation and rates of metabolism (see below).

B. Climate and Hydrology

Within both tropical and temperate zones, there is great variability in climate from arid to humid, and in topography from plains to mountain ranges. However, at the regional scale, far more precipitation falls on the land in the tropics than in the temperate zones (Dai and Trenberth, 2002), and runoff in terms of precipitation minus evaporation is highest (ca. 2000 mm on average) in the tropics. In the southern temperate zone, runoff is also quite high (ca. 1500 mm) due to orographic rain on the west coasts of New Zealand and South America. In the northern temperate zone, it is consistently lower than in the tropics (<1200 mm, Baumgartner and Reichel, 1975). Regionally, tropical climates are dominated by the high inputs of solar radiation which cause rapid evaporation from terrestrial and aquatic surfaces. This, coupled with the typically high rainfall intensity, characterizes the Intertropical Convergence Zone between the trade wind systems on either side of the equator. When large amounts of water vapour that have evaporated from warm tropical oceans condense into heavy rain, latent heat energy is released, increasing turbulence and generating the violent storms emblematic of much of the tropics. The Intertropical Convergence Zone does not form a continuous belt but, instead, fills and reforms to produce a chain of major disturbances, causing variable rainfall and alternating patterns of flooding and droughts throughout the equatorial tropics (Pereira, 1989; see also Chapter 1 of this volume).

Most large tropical rivers experience predictable seasonal floods of great magnitude (Balek, 1983, Dudgeon, 1999a, 2000; Arrington and Winemiller, 2006). Monsoon systems operate in

the tropics over Asia, northern and western Africa, northern Australia, and in the Americas as annual cycles of wet and dry seasons (Webster *et al.*, 1998). The rainy season occurs when warm, moist winds move inland from the warm oceans whilst the dry season eventuates when cold, dry winds blow from temperate lands locked in winter. However, unpredictable and damaging floods may arise from hurricanes, typhoons or cyclones (Balek, 1983; Covich *et al.*, 2006) which, although mainly tropical, occasionally affect subtropical and temperate zones. Monsoon intensities, especially in Asia, are linked ('teleconnected') with the El Niño-Southern Oscillation phenomenon, and it is largely the strength of ENSO events that governs the strength of the monsoons (Jury and Melice, 2000). Strong and persistent ENSO events may give rise to devastating droughts in Africa, Southeast Asia, and Australia while causing floods in parts of China, Europe and the Americas (Davis, 2001).

Of the 12 greatest river drainages on Earth, ranked in terms of discharge ($>415 \text{ km}^3 \text{ yr}^{-1}$), six are tropical, with the highest being the Amazon with a mean annual discharge of $6642 \text{ km}^3 \text{ yr}^{-1}$, followed by the Congo at $1308 \text{ km}^3 \text{ yr}^{-1}$ (Dai and Trenberth, 2002; Table I). After proportional correction for drainage area, all tropical river drainages except the Congo have higher runoff than temperate rivers. Another outlier, the Brahmaputra [lat. 25.2°N], probably should be grouped with the tropical river systems on the basis of runoff per unit area of catchment; Table I). At least as far as large rivers are concerned, annual flow variability tends to be only marginally lower in the tropics than in temperate zones (McMahon *et al.*, 1992). This lack of marked difference is important because claims of a 'more predictable' flow environment in the tropics (e.g. Junk and Welcomme, 1990) must be treated with caution in the context of considering a wide range of tropical climates and inter-annual variability at the scale of whole drainage networks. Even non-seasonal streams in humid tropical areas can be subject to occasional drought, with concomitant impacts on the aquatic biota (Covich *et al.*, 2003, 2006). The primary issue here is that of stream size; even where rainfall is generally highly seasonal, flows will follow predictable patterns in large rivers but remain flashy and relatively unpredictable in the headwaters (see Section V). While much of the present chapter focuses on comparing tropical and temperate stream ecosystems because that is where the majority of research has been done, there are obvious ecological differences associated with river size (e.g. Stanley and Boulton, 2000). Some of these will be exaggerated in wide tropical rivers

TABLE I Top 12 River Basins on Earth, Ranked Based on Discharge at River Mouth (from Dai and Trenberth, 2002)

River basin	Discharge ($\text{km}^3 \text{ yr}^{-1}$)	Drainage area (1000 km^2)	Discharge/drainage area	Latitude	Location
Amazon	6642	5854	1.135	2	Obidos, Brazil
Congo	1308	3699	0.354	4.3	Kinshasa, Congo
Orinoco	1129	1039	1.087	8.1	Pte Angostu, Venezuela
Yangtze (Chang Jiang)	944	1794	0.527	30.8	Datong, China
Brahmaputra	628	583	1.078	25.2	Bahadurabad, Bangladesh
Mississippi	610	3203	0.190	32.3	Vicksburg, Mississippi, USA
Yenisey	599	2582	0.232	67.4	Igarka, Russia
Paran	568	2661	0.213	32.7	Timbues, Argentina
Lena	531	2418	0.220	70.7	Kusur, Russia
Mekong	525	774	0.678	15.1	Pakse, Laos
Tocantins	511	769	0.665	3.8	Tucuruí, Brazil
Tapajos	415	502	0.827	5.2	Jatoba, Brazil

The ratio of volume to drainage area indicates runoff. Tropical rivers are in bold.

where higher water temperatures and insolation can enhance plant productivity and microbial respiration (as described below).

River drainages also may be characterized by their annual flow regimes. Using a global database of monthly flows in 969 streams, Haines *et al.* (1988) identified 15 different river flow regimes. In the Asian-Australian monsoonal regions, they found streams with flow peaks in mid- or late-summer (Groups 6 and 7 respectively) whereas rivers with peak flows in autumn (Groups 9, 10 and 11) occur in Africa, central and southern America, and Southeast Asia. Conversely, streams in the cold temperate zones with a snow season tend to have flow peaks in late spring and early summer (Groups 2, 3 and 4) and streams of the warm temperate zones have flow peaks in autumn, winter, and early spring (Groups 11, 12, 13, and 14). While descriptors from temperate zones such as 'autumn' or 'spring' cannot have exact equivalents in tropical latitudes (and so should be interpreted with caution), this monthly analysis reveals distinct differences in the annual flow regimes between tropical- and temperate-zone rivers at a broad scale, related to latitudinal climatic patterns and the timing of peak discharge.

Puckridge *et al.* (1998) explored patterns of flow variability in more detail, assessing 23 measures of hydrological variability for 52 large river drainages worldwide, with approximately equal numbers of gauging stations in arid, temperate, tropical, and continental climatic regions. They identified groups of river systems along a spectrum from 'tropical' to 'dryland'. However, some river drainages from continental climates occurred at both extremes of the range, illustrating the limitations of even this quite complex analysis. For example, Central African river drainages from wet tropical climates (Oubangu [Ubangui], Sanaga, and Niger) shared the lowest variability scores with those from continental and/or polar climatic influences (Neva, Fraser, and Idgirka). Puckridge *et al.* (1998) emphasize that each river system appeared to have its own 'signature' of flow regime that was masked by efforts to combine the collective measures of hydrological variability in their analysis. Nonetheless, a significant association between the vectors of flow variability and climate remained and, on most measures of hydrological variability, tropical river drainages tended to be significantly lower than their equivalent-sized temperate counterparts (Puckridge *et al.*, 1998).

Do different patterns in hydrology result in ecological differences between tropical and temperate river systems? Is the relatively predictable flow regime, even in the seasonal wet-dry tropics, likely to have repercussions on biodiversity and ecological processes? Tropical and temperate regions are both drained by large-river drainages that, in the unregulated and unconstrained state, have large seasonal floods (Dudgeon, 2000; Arrington and Winemiller, 2006). This 'flood pulse' may be more marked and predictable in some tropical rivers due to the extended wet season, leading Junk *et al.* (1989) to propose the flood pulse concept which asserts that regular pulses of river discharge largely govern the dynamics of river-floodplain systems. The flood pulse concept has been criticized for focusing on over-bank flows and for understating the significance of spatial and temporal flow variability in rivers within other climatic regions (e.g. Walker *et al.*, 1995b; but see also Junk and Wantzen, 2004). This is an interesting reversal of the usual case when models established in the north-temperate zone are applied to tropical streams. Floods play central roles in ecosystem replenishment and disturbance, regardless of climatic zone (Dodds, 2002; Woodward and Hildrew, 2002), and the extent to which these differ between tropical and temperate streams is discussed below (see Section V).

III. BIODIVERSITY AND ENDEMISM

A. Different Scales of Biodiversity

Latitudinal gradients of diversity have been discussed for more than a century (Hawkins, 2001). Most groups of organisms are more diverse in the tropical oceans and on land; only

a few groups peak in diversity in temperate zones (e.g. cambarid and astacid crayfishes, Plecoptera, simuliid blackflies, salmonid fish) or show no evident latitudinal gradient (e.g. stream macrophytes; Crow, 1993; Jacobsen and Terneus, 2001). For many groups, the latitudinal gradient has been persistent and is clearly evident in fossil assemblages (Buzas *et al.*, 2002). While it is widely accepted that diversity is highest in the tropics, little is known about the reasons underlying this pattern or the variability within and among groups and at different scales of local and regional diversity. Understanding the mechanisms responsible for this difference might shed light on ecological differences between tropical and temperate streams.

Diversity gradients in fresh water have received much less attention than marine or terrestrial environments (Boyer, 2002). Comparisons of diversity have been hampered by the imbalance in research effort between these climatic zones. For example, lists of species are scarce for the tropics – especially for macroinvertebrates – and the identification of tropical species has been difficult for non-specialists. Freshwater assemblages comprise a diverse mix of taxa that have invaded fresh waters independently, following different biogeographical patterns, which may well explain why overall latitudinal diversity gradients for these organisms are obscure (Heino *et al.*, 2002).

Diversity can be viewed at two scales – local (alpha diversity) and regional (gamma diversity) – that are usually strongly related across different taxa and continents (Caley and Schluter, 1997). Typically, a larger regional pool of species is reflected in greater species richness at the local site scale. Where site richness does not increase with regional richness, some form of ecological limitation is suggested (Craig, 2003). A direct relationship between local and regional diversity is apparent in stream fishes (Angermeier and Winston, 1998) and Odonata (dragonflies and damselflies; Caley and Schluter, 1997). Frequent and/or intense disturbance, which is a prevailing feature in most streams (Flecker and Feifarek, 1994; Dodds, 2002), might limit the number of species coexisting locally, irrespective of regional diversity. On the other hand, the high capability for dispersal of aquatic insects (by flying or drifting) suggests that their species richness should be primarily under regional control (Heino *et al.*, 2002). It is therefore convenient to examine local and regional diversity separately.

B. Latitudinal Gradients in Local Diversity in Streams

Published comparisons of diversity among streams have typically been based on small numbers of samples, and have failed to show consistent latitudinal patterns. For example, Patrick (1964) suggested that tropical American streams were no more species-rich than their temperate counterparts, but Stout and Vandermeer (1975) arrived at the opposite conclusion based on an analysis of taxonomic units rather than biological species. Flowers (1991) found high variability in species richness between streams in Panama and concluded that, when this variation is more thoroughly documented, it may swamp any 'latitudinal gradient' in aquatic insect diversity. Comparisons among detailed studies suggest that diversity in the tropics is greater (e.g. Bishop, 1973; Pearson *et al.*, 1986; Smith and Pearson, 1987; Table II) or lower (Arthington, 1990) but are hindered by lack of standardization of methods used.

A rare example of the application of standard methods across a large latitudinal gradient is Lake *et al.* (1994) who sampled Australian temperate and tropical streams with the specific aim of comparing species richness. They used identical methods to sample stones at each site, and focused on streams that were very similar in geomorphology. Their conclusion was that the tropical streams did have greater species richness of aquatic insects. Although the contrast was statistically significant, the difference was neither large nor consistent among taxa. Interestingly, the sample units (stones) supported no more species in the tropical than in the temperate streams. However, in the tropics, as each new stone was sampled, species continued to be added beyond the limit in temperate streams such that an asymptote in the species versus area curve

TABLE II Conclusions Drawn by Ecologists Comparing Biota and Ecosystem Processes between Temperate and Tropical Streams

<i>Response variables</i>	<i>Comparative trend</i>	<i>Reference</i>
<i>Diversity, richness and community composition</i>		
Fungal communities on submerged wood	Higher fungal diversity on submerged wood in tropical streams; distinct fungal communities occur on wood in tropical, subtropical and temperate streams	Hyde and Goh (1999); Ho <i>et al.</i> (2001)
Blackfly (Simuliidae) species richness	Greater species richness in temperate streams	Hamada <i>et al.</i> (2002); McCreadie <i>et al.</i> (2005)
Species richness of Chironomidae (Diptera)	About 1.8 times more chironomid species, on average, in tropical streams	Coffman and de la Rosa (1998)
Chironomidae species richness in acid streams	Higher species richness of chironomid midges in tropical acid streams than equivalent temperate streams	Cranston <i>et al.</i> (1997)
Decapod diversity and ubiquity	Decapod crustaceans such as prawns and crabs are more diverse and widespread in tropical streams	Covich (1988); Dudgeon (1999a)
Representation of Plecoptera (stoneflies)	Lower abundance and diversity of Plecoptera in tropical streams	Vinson and Hawkins (2003)
Invertebrate species richness and water temperature	Similar relationship between insect species richness and maximum water temperature but two to fourfold higher species richness in lowland streams	Jacobsen <i>et al.</i> (1997)
Invertebrate species diversity on rocks	More rock-dwelling invertebrates in tropical Australian streams than in Australian temperate streams	Pearson <i>et al.</i> (1986); Lake <i>et al.</i> (1994)
<i>Habitat selection and behaviour</i>		
Food exploitation behaviour of shredders	No difference in feeding behaviour or preference for conditioned leaves between shredders from tropical and temperate streams	Graça <i>et al.</i> (2001)
Importance of woody debris to fish communities	As in temperate streams, addition of woody debris to pools in a tropical stream promoted fish species richness and abundance	Wright and Flecker (2004)
Size-based predator avoidance behaviour	As in temperate streams, multiple prey species in a tropical stream showed predator avoidance behaviour to large fish	Layman and Winemiller (2004)
Eel growth and behaviour	Eelers (<i>Anguilla marmorata</i> : Anguillidae) in a tropical stream grew faster and migrated sooner than in temperate streams	Robinet <i>et al.</i> (2003)

(continued)

TABLE II (continued)

<i>Response variables</i>	<i>Comparative trend</i>	<i>Reference</i>
<i>Macroinvertebrate life histories and production</i>		
Larval development times for insects	All 35 tropical species examined had faster total development times than (typically univoltine) life histories of temperate stream counterparts	Jackson and Sweeney (1995)
Insect emergence from streams	No differences in community composition at order level of insects emerging from temperate and tropical streams	Freitag (2004)
Seasonal regulation of life cycles of Chironomidae	Life-cycles of tropical chironomids are much less seasonally regulated than temperate species	Coffman and de la Rosa (1998)
Gross primary production	Relatively high in tropical rivers given low nutrient concentrations, likely to be extremely rapid rates of nutrient cycling	Cotner <i>et al.</i> (2006)
Secondary production of benthic insects	Abundance, biomass and secondary production in a tropical stream were low compared with temperate streams but in some tropical streams population turnover is rapid and larval growth may be very fast	Ramírez and Pringle (1998); Salas and Dudgeon (2002, 2003)
<i>Stream metabolism and organic matter processing</i>		
Stream metabolism and organic matter dynamics	Net ecosystem production correlated with photosynthetically active radiation and both tropical and temperate streams acted as net sinks of organic matter	Mulholland <i>et al.</i> (2001)
Responses of macroinvertebrate functional feeding groups to changes in food availability	In tropical streams in New Guinea and Hong Kong, responses of population density and relative abundance of some functional feeding groups to changes in riparian conditions and algal and detrital food availability were weaker than described for temperate streams	Dudgeon (1988, 1994)
Use of allochthonous foods by Ephemeroptera nymphs	Based on carbon and nitrogen stable-isotope ratios, mayflies in tropical streams assimilate allochthonous food sources more than in temperate streams	Salas and Dudgeon (2003)
Pathways of leaf litter breakdown in streams	Leaf litter breakdown is facilitated by shredders in some temperate streams but as shredders are often rare in tropical streams, a greater role may be played by microbial activity, enhanced by high water temperatures	Irons <i>et al.</i> (1994); Dudgeon and Wu (1999); Bass (2003)

(continued)

TABLE II (continued)

<i>Response variables</i>	<i>Comparative trend</i>	<i>Reference</i>
Proportion of herbivorous fish	Herbivorous fish species represent a greater proportion of the total fish community in tropical than temperate streams	Wootton and Oemke (1992)
Primary energy source for metazoan consumers	Stable-isotope data show that autochthonous primary production entering food webs via algal-grazer or decomposer pathways is the primary annual energy source for consumers in some tropical and temperate streams larger than third order	Thorp and Delong (2002)
Trophic guild representation	Tropical and temperate streams contain the same trophic guilds but some tropical streams have relatively lower densities of macroinvertebrate shredders	Bass (2003)

For further discussion and examples, see text.

(i.e. cumulative species by stones) was achieved at a greater number of stones, and therefore species, in the tropics (Lake *et al.*, 1994).

In another study that used standardized methods, Jacobsen *et al.* (1997) found that lowland tropical streams in Ecuador had more taxa than temperate lowland streams in Denmark whereas highland Ecuadorian and Danish upland streams shared very similar richness (see also Chapter 8 of this volume). The number of insect orders and families increased with maximum stream temperature, and therefore decreased with altitude and latitude. Although this study did not involve a latitudinal gradient of the type investigated by Lake *et al.* (1994), a compilation of published data (Jacobsen *et al.*, 1997) confirmed the relationship with temperature, which may result from a direct temperature effect on speciation, combined with geological history and/or climatic changes (Jacobsen *et al.*, 1997).

It would be expensive to replicate comparisons of taxon richness at many sites across a broad latitudinal gradient. Consequently, sampling at multiple sites has usually been confined to comparisons within major biogeographic regions. Only when the numbers of samples are high enough to encompass within-region variations do such comparisons become convincing. Vinson and Hawkins (2003) have produced the most comprehensive global study of stream invertebrate diversity to date, based on a compilation of data from 495 published estimates of local generic richness of several orders of aquatic insects. They used strict criteria to ensure reliability of diversity estimates, adopting only studies with substantial sampling effort. They restricted their analyses to numbers of genera and to the EPT orders (Ephemeroptera, Plecoptera and Trichoptera), because most studies identified these three taxa to genus and generic identifications are more frequently used than species-level identifications. The results revealed substantial site-to-site variation in richness within realms and biomes. However, the general pattern of richness, and especially the maxima from each region and biome, is quite clear. The summary of findings of Vinson and Hawkins (2003) are set out below:

- Generic richness of Ephemeroptera has peaks at 30°S, 10°N, and 40°N
- Generic richness of Plecoptera peaks at 40°N and 40°S
- Generic richness of Trichoptera is less variable but highest near the equator and 40°N and 40°S

- Richness of EPT taxa declines with increasing elevation, except for Plecoptera
- Maximum richness of EPT taxa increases with estimates of net primary productivity and declines with disturbance
- EPT orders have large variation in richness from site to site within latitudinal realms, but highest richness is recorded in broad-leaf forest biomes
- There is no consistency in the diversity of EPT orders across realms: for example, diversity of Ephemeroptera is highest in the Afrotropical realm; diversity of Plecoptera is highest in the Nearctic; and diversity of Trichoptera is highest in Australia.

These trends reveal numerous biogeographic patterns that potentially confound comparisons of latitudinal gradients (Craig, 2003), and mean that taxonomic comparisons of latitudinal patterns among continents must be made cautiously. However, in some regions, detailed knowledge of insect taxa within continents enables valid comparisons. For example, in Australia, apparently low diversity in Ephemeroptera and Plecoptera contrasts with higher diversity of Trichoptera and Diptera (Lake *et al.*, 1986). In streams of the Queensland Wet Tropics bioregion, Trichoptera are very diverse (Benson and Pearson, 1988; Walker *et al.*, 1995a), as are Chironomidae (Diptera) at the local scale (Pearson *et al.*, 1986) although their species richness is not exceptionally high at the regional scale and does not follow any latitudinal gradient (Cranston, 2000; McKie *et al.*, 2005). In a study of 394 Nearctic and 138 Neotropical sites, McCreadie *et al.* (2005) reported a greater richness of blackflies (Simuliidae) in temperate streams. As regional richness rose, local diversity reached an asymptote where further increases in regional richness did not match increases in local diversity (McCreadie *et al.*, 2005).

Where local site diversity and regional diversity are uncorrelated, then resolution of the issue of whether species richness is higher in the tropics becomes confounded by the interaction between evolutionary/biogeographic processes and local ecological and/or stochastic processes (Craig, 2003). Local diversity is a subset of regional diversity. Regional and historical processes can be important determinants of local patterns of diversity because they determine the characteristics of the species pools from which local communities can be assembled, and they set the upper limit on local species richness (Caley and Schluter, 1997). However, local diversity also depends on a hierarchical framework of multiple spatio-temporal scales (Boyero, 2003), each with an array of physical and biotic factors that can limit diversity (Angermeier and Winston, 1998). Tonn *et al.* (1990) proposed a conceptual framework of environmental 'filters' that represent the processes acting at different spatio-temporal scales that sequentially reduce the regional pool of species to a subset that occur locally. In streams, these filters might include flow regime and associated habitat characteristics (Poff and Ward, 1989) that determine the habitat templet (Townsend and Hildrew, 1994), as well as historical and biogeographic factors such as temporal and spatial isolation (Covich, 1988; Craig, 2003).

C. Latitudinal Gradients in Regional Diversity in Streams

With increasing taxonomic work in tropical regions, it is becoming feasible to use cumulative records of species number to compare between regions. For example, Boyero (2002) was able to compare species lists for different major regions from North to South America, and found much higher diversity in Central America despite the fact that taxonomic effort is likely to be less in Central America than North America. Such data on species per unit area could be biased by large differences in the area of the regions, but plotting richness data against area of the region and examining the deviations from the regression line (i.e. residuals) is informative (Rosenzweig, 1997). Plots of combined American and Australian data for Ephemeroptera indicate that the main positive outlier is Central America, confirming that it has higher richness (Fig. 1). Further support for this approach can be drawn from the fact that the end-points (Tasmania and North America) have well-described faunas whereas two regions with

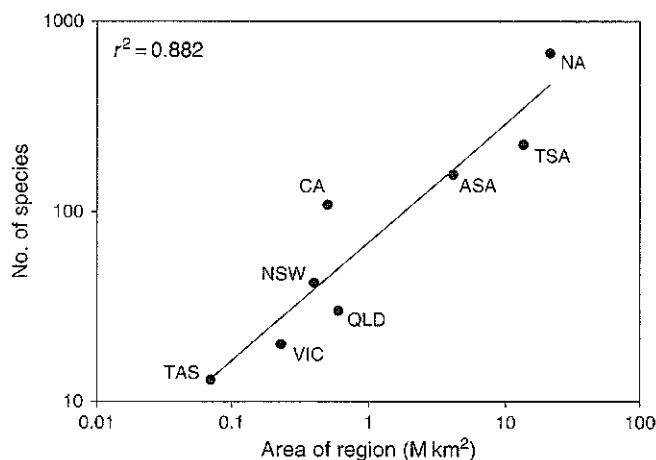


FIGURE 1 Species-area relationship for Ephemeroptera from different regions in the Americas and Australia (R. G. Pearson and L. Boyero, unpublished observations). Region abbreviations: ASA, Austral South America; CA, Central America; NA, North America; NSW, Coastal New South Wales (Australia); QLD, Coastal Queensland (Australia); TAS, Tasmania (Australia); TSA, Tropical South America; VIC, Victoria (Australia).

negative residuals (Queensland and tropical South America) have incompletely described faunas (Christidis, 2003). It is probable that the pattern would vary somewhat among different taxa; for example, Trichoptera and Diptera are particularly diverse in Australia (Pearson *et al.*, 1986; Lake *et al.*, 1994). Using the same approach, Odonata yield a similar trend to Ephemeroptera with tropical regions showing positive deviations from the regression line whereas the negative deviations are represented by temperate data sets (Fig. 2). Relative to its size, Central America apparently has the greatest species richness of these insect orders among the regions studied, and the data from each order represent an independent test of the hypothesis that tropical regions have higher richness of freshwater biodiversity.

Latitudinal trends in regional species diversity may also be asymmetrical. Boyero (2002) compiled total family, generic, and species richness data for Odonata and Ephemeroptera in four

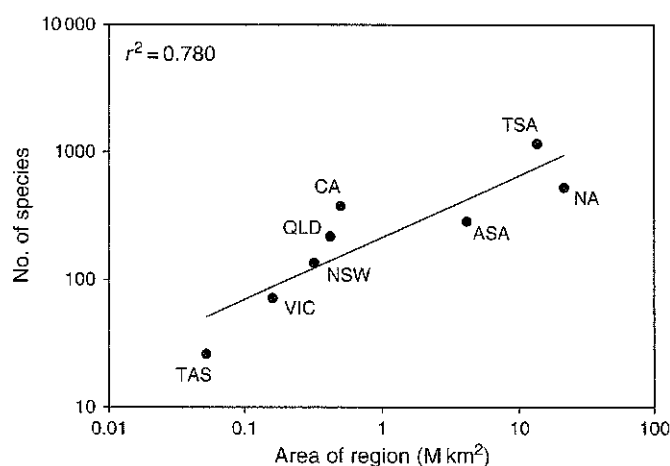


FIGURE 2 Species-area relationship for Odonata from different regions in the Americas and Australia (R. G. Pearson and L. Boyero, unpublished observations). For abbreviations, see Fig. 1.

large zones in the New World: temperate North America, tropical Central America, tropical South America, and temperate South America. The data were then standardized by total area. At all taxonomic levels, the richest zone was Central America with tropical and temperate South America being richer than temperate North America, implying asymmetrical diversity gradients. Clearly, more information is needed from a wider range of geographic regions and a greater variety of taxa, especially non-insect forms since it is clear that some freshwater groups (e.g. decapod crustaceans) are predominately tropical whereas others (isopod and amphipod crustaceans) are mainly temperate.

The detection of regional diversity gradients in riverine fish is easier than for macroinvertebrates due to the relative lack of taxonomic problems, the availability of many good data sets, and the ability to standardize comparisons. Fish species richness, either within continents or globally, is significantly correlated with total surface area of drainage basins and mean annual discharge (Welcomme, 1985; Oberdorff *et al.*, 1995) and also with net primary productivity, using estimates of terrestrial primary productivity as a surrogate for aquatic primary productivity (Oberdorff *et al.*, 1995). The slope of the line relating fish species richness to drainage-basin area is steeper for tropical rivers than temperate rivers (Amarasinghe and Welcomme, 2002), perhaps reflecting the greater per-unit-area richness of stream fishes in the tropics. Stream frog assemblages in New Guinea appear to have a limited number of species (usually about five), but different streams have different complements of species (S. J. Richards, James Cook University, personal communication). Therefore, frog diversity is not particularly high at the local site level, but moving from site to site greatly increases the cumulative number of species. This parallels the higher stone-to-stone accumulation of invertebrate species in the tropics compared to temperate streams (Lake *et al.*, 1994). Overall, these studies indicate regionally high biodiversity but not necessarily local maxima in tropical streams. If functional redundancy is high (i.e. many different species can fill the same niche), it is possible that these differences in biodiversity do not translate into ecological differences between tropical and temperate streams.

D. Endemism in Tropical and Temperate Streams

Endemism is an inherent feature of patchy environments at a range of scales, regardless of latitude, and is common in streams in mountainous areas where altitudinal climatic gradients may restrict dispersal. Endemism might be hypothesized to be greater in the tropics because tropical mountains span a greater variety of biomes than temperate mountains of equivalent altitude. Even relatively low mountain systems can affect biogeography and endemism. For example, mountains in the Australian tropics are not high (maximum 1700 m asl) but do display high endemism in some groups such as the parastacid crayfish and marked gradients in diversity of Trichoptera (Pearson, 2005). Endemism may be high among many aquatic invertebrate groups in montane regions of Africa, particularly because they are geographically isolated from each other (e.g. Dobson, 2004), but our current poor taxonomic understanding of the region makes definitive statements premature. In contrast, the stream fauna of the Andes exhibits a relatively lower degree of endemism, probably because the mountains lie in a single range with a direct connection to the temperate zone of southern South America (for more information, see Chapter 8).

Geological habitat fragmentation also promotes endemism across oceanic islands. For example, endemism is high on Madagascar and the Caribbean islands. Madagascar is one of the 12 'megadiverse' countries that together harbour 70% of the Earth's plant and animal species (McNeeley *et al.*, 1990), and approximately 90% of the island's freshwater species are endemic (Benstead *et al.*, 2000). Indonesia is also megadiverse, with over 900 species of amphibians and more dragonflies (over 660 species) than any other country (Dudgeon, 2000). The causes of endemism are probably the same across temperate and tropical latitudes, but the higher

regional species diversity typical of many freshwater groups in the tropics probably enhances opportunities for adaptive speciation, leading to higher levels of endemism. This hypothesis can only be tested adequately as taxonomic knowledge of tropical island stream biotas increases.

IV. FOOD-WEB ORGANIZATION

A. Trophic Structure and Taxonomic Representation

Many invertebrate taxa that dominate temperate streams are either rare or absent from streams in the tropics (Table II), and it is likely that such taxonomic 'gaps' may influence the trophic structure of stream food webs. For example, stoneflies (Plecoptera) are very diverse in the Nearctic and Palaearctic regions, including 17 European genera in northwest Africa north of the Sahara, and they also show a remarkable diversity in the Cape region of South Africa. However, across the rest of Africa, this order is represented by only a single genus, *Neoperla* (Perlidae). This low diversity is matched elsewhere in the tropics (Dudgeon, 1999a; Freitag, 2004) and raises the issue as to whether other groups expand to fill the trophic niches typically occupied by stoneflies, or whether the food webs of some of these tropical streams differ from their temperate counterparts – for instance, in terms of their dependence on inputs of riparian leaf litter (see also Chapter 3 of this volume).

Stoneflies are important across all feeding guilds in the Holarctic region where the mayfly family Baetidae, despite its high species richness, is dominated by grazers. However, in tropical Africa, the Baetidae has diversified into a wide variety of feeding guilds not occupied by them in the temperate zone, apparently exploiting the niches unfilled by Plecoptera. For example, there are several tropical genera of predatory baetids (e.g. Lugo-Ortiz and McCafferty, 1998) and at least one shredding genus (Dobson *et al.*, 2002). Evidently some taxa can adapt to vacant niches with the consequence that trophic structure of food webs is fundamentally the same in tropical and temperate streams (Table II), although 'trophic replacement' may involve different groups. The increased diversity of tropical Odonata mentioned earlier could also offer the possibility that members of this predatory order could occupy the niche vacated by the scarcity of large, carnivorous Plecoptera.

The same type of trophic group replacement in tropical streams has been shown for tadpoles. Amphibians are abundant and diverse in the humid tropics, and have been shown to directly influence the availability of algal resources and density of primary consumers (Ranvestel *et al.*, 2004). Studies of tropical stream communities have documented the role of tadpoles as 'ecosystem engineers' and shown how different species serve as detritivores (Flecker *et al.*, 1999) or as grazers that modify benthic habitats used by other species. Wootton and Oemke (1992) experimentally manipulated fish grazing pressure to determine the importance of herbivory by fishes in a Costa Rican stream, reporting that fish reduced macrophyte abundance and periphyton biomass. They concluded that because herbivorous fish species generally represent a larger proportion of the total fish community in tropical streams, they will have a more significant influence on plant and animal abundance than is the case in equivalent temperate habitats. The generality of these results has yet to be demonstrated, but it is notable that tropical streams contain fish functional groups, including specialized benthic herbivores such as Loricariidae (Neotropics) and Balitoridae (Asia) and certain Cyprinidae (e.g. *Garra* spp. in Asian and Africa) that are absent from temperate streams (for details, see Chapter 5 of this volume). It is not yet clear whether these different trophic pathways through fish and tadpoles in tropical streams alter rates of nutrient recycling or other functional processes, and this topic warrants more research (see McIntyre *et al.*, 2007). It also raises questions about functional redundancy and resilience to disturbance; we were unable to find studies comparing these between tropical and

temperate streams and rivers, despite the widespread concern over declining populations of amphibians in many regions (Stallard, 2001).

The detrital pathway is the primary source of energy in most heterotrophic streams (Dodds, 2002), and has received substantial attention in temperate systems. In tropical streams, it would be expected that relatively high plant productivity would increase the supply of plant detritus, with consequent effects on detritivorous species that provide essential ecosystem services (e.g. decomposition of organic matter, recycling of nutrients). In this regard, it is significant that when Rosemond *et al.* (1998) used underwater electric fields to exclude macroconsumers feeding on leaf packs in a stream in Costa Rica, an increase in invertebrate densities (mainly collector-gatherers) on leaf packs was not accompanied by any change in decay rates. This result is opposite to what has been observed in temperate streams where insect predators have been shown to control shredder densities and hence leaf pack breakdown rates (e.g. Oberndorfer *et al.*, 1984; Malmqvist, 1993). These observations support the hypothesis that leaf decay in tropical streams may be driven primarily by factors such as microbial activity rather than insect shredding (Rosemond *et al.*, 1998, Table II), and this seems borne out by the apparent paucity of insect shredders in many tropical streams (but see Section V). The matter is discussed in more detail in Chapter 3 of this volume.

Some investigators take the view that the process of leaf breakdown in tropical and temperate streams is similar (Benstead, 1996), despite the fact that macroconsumers eating plant material are much more common in tropical streams (Flecker, 1992; Wootton and Oemke, 1992); this might be interpreted as another example of the trophic replacement described earlier. Omnivorous fish (e.g. Characidae, Cichlidae and Poeciliidae) and shrimps (e.g. Atyidae, Xiphocarididae, and Palaemonidae) play major roles in leaf breakdown in some tropical streams where insect shredders are scarce or absent, as in some Puerto Rican (March *et al.*, 2001, Wright and Covich, 2005) and Costa Rican streams (Pringle and Hamazaki, 1998), while freshwater crabs have a similar function in Kenyan streams (Dobson *et al.*, 2002, Dobson, 2004). Insect shredders are reported to be numerically important in some other tropical streams, such as in Panama (L. Boyero, personal observations), Costa Rica (Benstead, 1996) and the Australian wet tropics (Cheshire *et al.*, 2005), where these insects (especially the Leptoceridae and Calamoceratidae) make a potentially important contribution to litter breakdown (Bastian *et al.*, 2007).

B. Food-Web Compartmentalization in Tropical and Temperate Streams

As we saw earlier for the hydrological comparisons, generalizations across tropical and temperate streams must take into account the spatial scales and sizes of lotic systems, and this need for appropriate scaling is equally true for trophic structure and food webs. In many tropical streams, steep waterfalls limit fish access to headwaters in coastal drainages (Covich *et al.*, 2006). These forested streams are dominated both numerically and in biomass by diverse species of omnivorous decapods (Crowl and Covich, 1994, Covich *et al.*, 2003) that carry out a range of trophic roles and whose activities also influence rates of organic-matter breakdown and primary productivity in ways not evident in temperate streams. Low-elevation tropical rivers have a high number of fish species, which tend to displace shrimps and have partially radiated to fill their niches. Along these tropical streams, the landscape imposes a type of food-web compartmentalization, with predation from fish having large impacts on invertebrates at low elevations whereas invertebrates dominate energy flow at middle and upper elevations, above barriers to fish dispersal. Although such distinct compartmentalization has yet to be described for temperate streams, and it may not be a special feature of tropical streams (Layman and Winemiller, 2004; see also Table II), the importance of decapods and greater functional diversity of fish at lower latitudes could give rise to some thus far unperceived differences in stream function.

V. PRODUCTIVITY, ORGANIC MATTER DYNAMICS, AND OTHER ECOSYSTEM PROCESSES

A. Productivity

Productivity in permanently-flowing tropical streams might be anticipated to be higher than that in equivalent temperate streams because continuously high temperatures allow year-round growth of both aquatic and surrounding terrestrial vegetation, while the persistent presence of water in many permanent streams reduces the impact of rainfall seasonality. Consistent high levels of insolation lead to continual primary production. In contrast, productivity in permanent temperate streams occurs mainly in spring and summer, and so total annual production is predicted to be less in equivalent-sized streams. In a comparison of stream metabolism among biomes in North America using directly comparable methods (Mulholland *et al.*, 2001), gross primary production was correlated most strongly with photosynthetically-active radiation, but was also limited by phosphorus. Highest primary production was measured in a temperate desert stream and productivity was least in a tropical stream (Quebrada Bisley, Puerto Rico). Although this stream had a closed canopy, shaded temperate streams included in the comparison study achieved higher gross primary productivities (Mulholland *et al.*, 2001). Other studies in tropical and temperate streams confirm that primary productivity is typically limited by light and nutrients, regardless of latitude (Pringle and Triska, 1991; Pearson and Connolly, 2000; Montoya *et al.*, 2006). Primary production in some well-lit tropical streams may be limited by intense herbivory that strongly suppresses autotrophic biomass (Ortiz-Zayas *et al.*, 2005). In such situations, even in full sunlight, community metabolism depends substantially upon allochthonous detritus from upstream forested stream reaches.

Secondary production in tropical streams is infrequently researched, making comparisons with temperate zones difficult. Macroinvertebrate abundance is often high in tropical streams, especially where fish predators are excluded by waterfalls (Covich, 1988; Covich *et al.*, 2006). When these high densities are combined with the more rapid turnover generally encountered in tropical freshwaters (e.g. Jackson and Sweeney, 1995; Ramírez and Pringle, 1998), secondary production would typically be expected to be higher than in temperate systems. At first glance, this appears to be not the case. In one of the few such studies, Ramírez and Pringle (1998) demonstrated that secondary insect production in Sábalo Stream, Costa Rica, estimated at $363.7 \text{ mg AFDM m}^{-2} \text{ yr}^{-1}$, was low compared with that in similar-sized temperate streams. They speculated that this was due to the low abundance of insects (a maximum of 2188 individuals per m^2) which was not typical of tropical streams, but a consequence of the high predation intensities at their study site where three species of omnivorous *Macrobrachium* (Palaemonidae) shrimps were abundant (Pringle and Hamazaki, 1998). Besides reducing insects by predation and competition (Ramírez and Hernandez-Cruz, 2004), these shrimps would also have made a significant contribution to macroinvertebrate secondary production. This has been shown to be the case elsewhere in the tropics (e.g. Bright, 1982; Mantel and Dudgeon, 2004; Yam and Dudgeon, 2006), and shrimp production may be a very significant proportion of total benthic production, especially in comparison with temperate streams where shrimps are absent. There have been few other studies of secondary benthic productivity in tropical streams, but there is some evidence of inter-year taxon-specific variation in production related to rainfall (Dudgeon, 1999b). A detailed account of macroinvertebrate production in tropical streams is included in Chapter 4 of this volume.

Many tropical stream insects are multivoltine and have rapid growth, short generation times, and high production: biomass ratios (e.g. Jackson and Sweeney, 1995; Salas and Dudgeon, 2002, 2003). This suggests that estimates of secondary production based on assumptions about univoltine life histories or uncritical application of standard methods for temperate streams will significantly underestimate production of tropical stream insects. However, high turnover rates do not always result in high production. Benke (1998) recorded that extremely high turnover

rates of chironomids in a subtropical river were matched by high net production. This could reflect short larval life spans and may be interpreted as a strategy for species living in streams frequently disturbed by floods, where mortality is high due to abiotic factors (Huryn and Wallace, 2000). This type of adaptation has been reported in tropical lowland rivers by Ramírez and Pringle (2006), and parallels the situation observed in frequently-disturbed streams in other climatic zones (e.g. desert streams in Arizona: Grimm and Fisher, 1989).

B. Organic Matter Dynamics: Seasonal Inputs and Instream Litter Retention

In forested tropical streams, as in the temperate zone, allochthonous inputs of detritus are typically the major source of energy. Leaf-litter dynamics in all streams are determined by seasonality of leaf fall and by retention within river channels. Leaves entering the stream are conditioned by microbial colonists, and broken down by physical abrasion and the feeding activities of invertebrates, especially 'shredders' that are capable of comminuting coarse organic matter (> 1 mm in size, Cummins and Klug, 1979). This model of leaf breakdown is widely supported by studies in the north-temperate zone but does it hold true in humid and wet-dry tropical streams?

In deciduous forests of the north-temperate zone, leaf litter input is strongly seasonal, falling during a short period of time in the autumn, often associated with increased flows as rainfall increases (Dodds, 2002). In evergreen forests of the southern temperate zone, leaf fall is less seasonal although for many eucalypt species there is a distinct peak of litter drop in summer, coinciding with low or zero flows (Bunn, 1986). When flow resumes or increases, litter that has accumulated on the streambed is carried in a pulse and is now available to aquatic biota (Boulton, 1991). In the humid tropics, however, inputs via leaf fall may continue throughout the year (Benson and Pearson, 1993; Larned, 2000) and, coupled with the relatively stable flows, allochthonous organic matter supply is not as pulsed as in many temperate streams (see also Chapter 3 of this volume).

Conversely, in the wet-dry tropics, leaf fall often occurs at the beginning of the dry season when river flows are declining (Douglas, 1999), resembling the southern temperate streams described above. Again, this may leave large volumes of leaf litter sitting in the river channel for several months, until the rains return. Terrestrial breakdown processes including microbial conditioning and invertebrate attack are likely to be accelerated by the high temperatures typical of the tropics but fire may also be a significant factor, consuming the leaf litter but also enhancing litter fall through 'scorching'. For example, fires in the savannahs of the wet-dry tropics of northern Australia killed vines and woody species, reduced the canopies of surviving trees, and caused a shedding of leaves several days after the fire had passed (Douglas *et al.*, 2003). Although the effect was to increase the amount of leaf litter in the riparian zone and on the dry streambed, standing crops of leaf litter were still lower than in unburnt streams. However, in the burnt streams, the lack of vines and other retentive structures meant that litter was readily carried into the stream so that, after flow resumed, standing crops of organic matter in burnt streams exceeded those in unburnt streams. By the end of the flow phase, standing crops of benthic organic matter were similar between burnt and unburnt streams because the destruction of debris dams during the fire had reduced in-stream retention of litter, enhancing export from the burnt streams (Douglas *et al.*, 2003).

In-stream retention dynamics of leaf litter are expected to show no differences between tropical and temperate latitudes because of the overriding influences of flow patterns on export and retention (Brookshire and Dwire, 2003; see also Chapter 3 of this volume). Mathooko *et al.* (2001) demonstrated the importance of rocky outcrops, the stream edge, roots and particularly debris dams in capturing entrained leaves in the Njoro River, Kenya. These features have been highlighted as key retention structures in temperate streams (Speaker *et al.*, 1984, Webster *et al.*, 1987), and the same holds true for lateral transport and deposition

on tropical and temperate floodplains (Junk *et al.*, 1989, Jones and Smock, 1991; see also Chapter 7 of this volume). Similarly, Afonso and Henry (2002) identified the same relationship between retention and discharge in a Brazilian tropical stream as has been found in equivalent temperate streams, noting the loss of organic matter that occurs during high flows when retentive structures are submerged or carried downstream. Unfortunately, there is a dearth of studies of transport distance and deposition velocity of coarse particulate organic matter in tropical streams (see Table 4 in Brookshire and Dwire, 2003), which limits our ability to compare litter dynamics in tropical and temperate streams. The limited published information is summarized in Chapter 3 of this volume.

C. Organic Matter Dynamics: Biologically Mediated Breakdown

The prevailing model of leaf breakdown in streams emphasizes the central role played by microbes in 'conditioning' the litter and improving its palatability for detritivorous invertebrates, including shredders such as some tipulid larvae (Diptera), particular Plecoptera and Ephemeroptera nymphs, and certain case-building Trichoptera larvae (Dodds, 2002). Irons *et al.* (1994) proposed that microbial activity was the main determinant of processing rate at low latitudes whereas macroinvertebrates were more important at higher latitudes. The greater efficiency of microbial activity as a consequence of higher water temperatures therefore leads to higher breakdown rates in the tropics than in temperate regions (Irons *et al.*, 1994; see also Chapter 3 of this volume).

An apparent fundamental difference between tropical and temperate streams is the paucity of shredding invertebrate detritivores in many parts of the tropics. This is a widespread phenomenon, having been identified from Hong Kong (Dudgeon and Wu, 1999) and elsewhere in tropical Asia (Dudgeon, 1999a), New Guinea (Dudgeon, 1994; Yule, 1996), Central America (Rosemond *et al.*, 1998), Brazil (Walker, 1987), Colombia (Mathuriau and Chauvet, 2002) and East Africa (Tumwesigye *et al.*, 2000; Dobson *et al.*, 2002), although it is not true of tropical Australian rainforest streams (Pearson and Tobin, 1989; Pearson *et al.*, 1989; Nolen and Pearson, 1993; Cheshire *et al.*, 2005). This apparent absence of a feeding guild from much of the tropics – despite its importance in temperate streams – requires an explanation. The shredders that dominate the north temperate zone are concentrated into relatively few higher taxa, most notably certain Plecoptera and Trichoptera, plus amphipod crustaceans. These are taxa that probably evolved in cool running waters so one hypothesis to explain their absence from the tropics is a lack of tolerance for consistently high water temperatures (Irons *et al.*, 1994).

Shredders may be scarce or absent from tropical streams for several reasons that are not mutually exclusive. First, the biomass of detritus may be too low or its pattern of input too unpredictable to support viable shredder populations. Although very few estimates of leaf litter biomass and dynamics have been carried out in tropical streams, all suggest that detritus is at least as abundant as in equivalent temperate streams (review in Dobson *et al.*, 2002; see also Chapter 3 of this volume). Secondly, increased microbial activity may also be a reason for reduced shredder numbers in the tropics (Irons *et al.*, 1994). If microorganisms and macroinvertebrates are in direct competition for a limiting resource, then consistently high temperatures may give the microbial component the competitive advantage. Although there are few data to support or refute this idea, Mathuriau and Chauvet (2002) demonstrated the high biomass of hyphomycete fungi in leaf litter decomposing in Colombia and, crucially, the rapid rate of accrual of this biomass. However, this hypothesis that microbes and macroinvertebrates are competing for resources would only apply if leaf litter inputs were low or highly pulsed; high microbial activity combined with a constant supply of fresh leaf litter would surely be advantageous to shredding invertebrates, as there would be a constant supply of conditioned detritus. Thus far, the evidence does not support the notion that competition from microbes limits the abundance of shredders in tropical streams (see also Chapter 3).

A third explanation is that the inputs are lower in quality than those in temperate zones because there are high concentrations of toxic compounds in the leaves of many tropical species (Wantzen *et al.*, 2002; see Chapters 3 and 7). The quality of leaf litter as a food resource for shredders can be estimated by its breakdown rate (Petersen and Cummins, 1974). Breakdown rates from the tropics are generally high (e.g. Dudgeon and Wu, 1999; Larned, 2000; Dobson *et al.*, 2004) and include the highest rates recorded in the literature (Irons *et al.*, 1994, Mathuriau and Chauvet, 2002). The relative palatability of leaf types in temperate and tropical zones has been compared using reciprocal feeding experiments (Graça *et al.*, 2001). In that study, *Alnus glutinosa* (Betulaceae) leaves from Germany and *Hura crepitans* (Euphorbiaceae) leaves from Venezuela were offered to European and South American shredders. All animals preferred conditioned over unconditioned leaves, and although the South American shredders preferred the temperate *Alnus* leaves, *Gammarus* amphipods from Germany did not distinguish between the leaf types. Furthermore, all shredder species grew significantly irrespective of the leaf species upon which they were fed. However, the German leaves were derived from a forest dominated by only two tree species, whereas the Venezuelan forest contained at least seven other riparian species (Graça *et al.*, 2001). Total shredder activity will be determined by the overall quality of leaf litter entering the channel, so the palatability of all common species needs to be assessed. Dobson *et al.* (2004) found that all the riparian leaf types decomposed rapidly in the Njoro River, Kenya, and hence were probably highly palatable. In an Australian stream, however, palatability has been shown to vary substantially among species (Pearson and Tobin, 1989; Nolen and Pearson, 1993; Bastian *et al.*, 2007), as would be expected in a system where there may be scores of species contributing litter to the stream since each may have various defences against terrestrial herbivores (Benson and Pearson, 1993). Palatability can also vary depending on whether the leaves come from the canopy or from the understorey, as the latter may be less well defended by secondary compounds (Downum *et al.*, 2001). In any case, whether leaf secondary compounds alter the relative importance or role of shredding macroinvertebrates in leaf decomposition in tropical streams is still unresolved (Wright and Covich, 2005).

A fourth explanation is that shredding taxa really are present, but have been overlooked. This hypothesis deserves more research because there is some evidence that some tropical taxa found on leaf packs are not normally associated with shredding elsewhere. For example, the baetid mayflies of the genus *Acanthiops* in the East African highlands are shredders (Dobson *et al.*, 2002), although baetids in north-temperate streams are grazers. More widespread are freshwater crabs, generally overlooked or significantly under-recorded by standard benthic sampling methods, are often extremely common, at least in sub-Saharan Africa, where they can account for 80% or more of the entire benthic invertebrate biomass (Dobson, 2004). Analyses of gut contents of several species of freshwater crabs have demonstrated that their diet is dominated by shredded detritus (Dobson, 2004). These figures are derived from a very small number of studies but if this pattern is consistent across the continent, then shredders, far from being rare, would be significantly more important in tropical Africa than in most temperate zones. Shrimps and fishes in tropical streams may also play key roles in processing leaf litter, and atyid and palaemonid shrimps which are abundant in almost all tropical streams may be especially important in this regard. For example, in Puerto Rican streams, leaf litter decomposes rapidly in the presence of shrimps (Crowl *et al.*, 2001; March *et al.*, 2001; see also Chapter 4 of this volume). In Australia, parastacid crayfish are important consumers of leaf litter, including green leaves that are washed into rainforest streams during severe storms (J. Coughlan and R. G. Pearson, unpublished data).

Finally, it should be noted that the paucity of even 'typical' shredders in the tropics is not universal. For example, Graça *et al.* (2001) reported that two shredding caddisflies are abundant in streams in northern Venezuela, while Benstead (1996) recorded high densities of insect shredders in Costa Rican streams, albeit of only three taxa. In Queensland rainforest

streams in the Australian tropics, shredders also seem to be quite common (Cheshire *et al.*, 2005), and much litter processing is carried out by macroinvertebrates (Pearson *et al.*, 1989; Nolen and Pearson, 1993; Bastian *et al.*, 2007). These observations give some support to the hypothesis that shredders (especially crabs and shrimps) have been overlooked, partly because of expectations of the taxa that might be involved have been based solely on the ubiquitous model of leaf-litter processing developed in northern temperate systems.

D. Nutrient Cycling and Limitation

Most of our knowledge about nutrient cycling and limitation is derived from work in temperate streams. Effort has focused on phosphorus because this has been shown to limit primary production in many rivers (e.g. Fairchild *et al.*, 1985; Pan and Lowe, 1994), including tropical streams (Pringle *et al.*, 1986; Larned and Santos, 2000). Although concentrations of nutrients in tropical streams are typically considered to be very low due to intensive weathering (as described earlier), geothermal activity in some streams such as those at La Selva, Costa Rica, increases phosphorus concentrations of in-welling groundwater, enhancing rates of microbial respiration (Ramírez *et al.*, 2003) but not necessarily affecting insect assemblage composition (Ramírez *et al.*, 2006). Where phosphorus enrichment of tropical streams has taken place, respiration rates can exceed those in the temperate streams (Webster *et al.*, 1995). Such differences in nutrient concentrations and their effects on microbial respiration arise from local factors such as groundwater inputs and catchment geology, and do not seem to be attributable to latitude.

Like phosphorus, nitrogen has been shown to limit or co-limit primary productivity in temperate (Hill and Knight, 1988), subtropical (Mosisch *et al.*, 2001), and tropical (Ramos-Escobedo and Vazquez, 2001) streams. Downing *et al.* (1999) suggest that nitrogen limitation is more common in the tropics, but nitrogen dynamics appear to be similar across temperate and tropical streams. The few studies undertaken with ^{15}N tracers in temperate streams (Mulholland *et al.*, 2000; Tank *et al.*, 2000) yield uptake rates of ammonium and nitrate comparable to those reported from Quebrada Bisley stream in Puerto Rico (Merriam *et al.*, 2002). Data are too scarce to generalize but differences in ^{15}N balance appear to be more related to stream retentiveness (lack of woody debris in the tropical stream) and size than to latitude. A similar conclusion was drawn by Webster *et al.* (2003): a comparison of ammonium uptake among streams at different latitudes in North America produced no statistically-significant relationships.

E. Responses to Natural Disturbances and Introduced Species

Many tropical streams experience cyclones and hurricanes (e.g. Covich *et al.*, 1991) as well as drought (Covich *et al.*, 2003, 2006), and these natural disturbances seem just as prevalent in temperate systems where their effects are broadly similar. For example, floods resulting from torrential rains during cyclones scour benthic plants and animals from headwater streams (Maltchik and Pedro, 2001) and redistribute sediments, whereas droughts cause differential mortality, localized crowding due to habitat contraction (Crowl and Covich, 1994), and a prolonged decrease in reproductive output of some taxa (Covich *et al.*, 2003). Rates of faunal and biogeochemical recovery also appear to be similar and rather swift (McDowell *et al.*, 1996; Shivoga, 2001), reflecting the adaptations of the local biota to the prevailing disturbance regime. Inhabitants of riffles in upland streams in the tropics experience a similar range of disturbances to those in temperate zones, although the intensity of tropical storms may reduce the predictability of events compared with, say, streams fed by snowmelt (Rosser and Pearson, 1995). Streams in the aseasonal tropics may experience a significant range of disturbances on a daily basis (Yule and Pearson, 1996).

There have been very few studies of disturbance in large tropical rivers although there are grave concerns about potential effects of dams and other hydrological alteration (Dudgeon,

2000; Pringle *et al.*, 2000b; Wantzen *et al.*, 2006). Ribbink (1994) assessed the role of natural disturbance in large tropical river basins, and showed that African river systems generally support low fish diversity, with the exception of the Congo. While this is partially due to the high habitat diversity of the Congo system, it also arises from its equatorial location. Dry seasons in one section of the catchment are countered by wet seasons in the other, resulting in a relatively constant flow in the main catchment area. In contrast, other major river systems beyond the equator exhibit greater seasonality and major fluctuations in discharge, so fishes must be opportunists adapted to frequent large-scale disturbance (Ribbink, 1994).

While the negative effects of exotic or introduced species on biota and ecosystem processes in temperate streams are well known (e.g. Allan and Flecker, 1993), responses to species introduced into tropical streams have been less documented although they appear to be similar. Processes such as litter decomposition that rely upon living organisms are susceptible to changes wrought by the introduction of alien species. For example, in eastern and southern Africa, Rainbow trout (*Oncorhynchus mykiss*: Salmonidae) was widely introduced into highland streams during the first half of the 20th century, often into streams that were previously fishless (see also Chapter 8 for discussion of trout in South America). Anecdotal evidence suggests that the arrival of trout led to a large reduction in density of crabs as a result of predation (see Dobson, 2004). As crabs appear to be key members of the detritus-processing guild (see above), depletion in their numbers would inevitably reduce processing efficiencies of organic matter. Conversely, the North American crayfish *Procambarus clarkii* (Cambaridae), introduced for aquaculture in various parts of Africa, has escaped into the wild and is gradually extending its range (Dobson, 2004). *P. clarkii* acts as a shredder in Hawaiian mesocosm studies and is more effective than native shrimps (Larned *et al.*, 2003). Other concerns over the introduction of *P. clarkii* include its effect in out-competing endemic crustaceans in locations where it has become abundant, such as the shrimp *Macrobrachium grandimanus* (Palaemonidae) in Hawaii (Larned *et al.*, 2003).

Theories that diverse communities are more resistant to invasions by introduced species are being challenged (Levine, 2000), and it seems that biodiverse tropical streams are no less susceptible than their temperate counterparts. Thus far, the impacts of invasive species on communities have been most severe on low-diversity systems including islands and highly disturbed habitats (Kolar and Lodge, 2001), although there are exceptions to this (e.g. Lake Victoria). Tropical streams face a number of threats from human disturbance (as described elsewhere in this volume, especially in Chapter 10) and their repercussions are likely to be at least as serious as those reported for temperate systems.

VI. CONCLUSIONS

Comparisons of temperate and tropical streams are confounded by immense variability inherent in these systems within these latitudes, and the wide range of climatic and hydrological conditions. Few robust generalizations can be made, and those that can are rather self-evident. Streams in the tropics typically receive higher insolation and more intense rainfall, have warmer water and often large predictable floods, and for many taxa, harbour higher biodiversity than their temperate equivalents. However, our review of the literature fails to reveal consistent differences in food-web structure, productivity, organic-matter processing or nutrient dynamics, and response to disturbance (Table II), and there is no persuasive evidence that the adjective 'tropical' has particular significance when applied to stream ecology. Instead, ecological processes in tropical streams tend to be driven by the same variables that are important in temperate ones. For example, biotic responses to drought and flooding are similar to those in temperate

streams while productivity is limited by the same variables of nutrients, shading, and trophic structure. Consequently, valid extrapolation of models and management strategies may not be so much an issue of latitude (tropical versus temperate) but of ensuring suitable comparability at an appropriate (stream) scale. This review demonstrates clearly that whereas ecological mechanisms may be similar, the organisms involved in ecological processes in tropical and temperate streams can and do differ. It will be necessary to progress beyond the taxonomic biases arising from the results of investigations undertaken in the temperate (particularly north-temperate) latitudes when trying to explain phenomena observed in tropical streams.

ACKNOWLEDGMENTS

We thank David Dudgeon, Alonso Ramírez, and an anonymous reviewer for useful comments that improved the final text. We are also grateful to our respective institutions for support and funding during the preparation of this manuscript.

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