



## STONEFLIES (PLECOPTERA) IN A TROPICAL AUSTRALIAN STREAM: DIVERSITY, DISTRIBUTION AND SEASONALITY

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### ABSTRACT

Stoneflies (Eustheniidae, Gripopterygidae) were light-trapped at 24 sites on small to large streams over a 300 m elevation gradient. Catches were small but 8 species occurred; jackknife estimates of total richness (8-11 spp.) suggest the species list is reasonably complete. Emergence patterns were weakly seasonal with apparent peaks in the warm, wet season. Some species ranged extensively along the elevation/stream size gradient but Canonical Correspondence Analysis supports the existence of a compositional gradient from lower, larger woodland streams to higher, smaller streams in rainforest. We suggest improvements in survey design for investigating stoneflies in tropical streams.

**Keywords:** Plecoptera, light traps, elevation gradient, stream network, survey design

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### INTRODUCTION

Relative to their temperate zone counterparts, tropical Plecoptera are incompletely understood. Stoneflies can be numerically (Bispo & Oliveira 2007) and functionally (Cheshire et al. 2005) important in tropical streams. However, stoneflies appear to be a significant exception to the general pattern of higher biodiversity in the tropics (Hillebrand 2004). Family and generic diversity decrease toward the equator (Zwick 2000; Vinson & Hawkins 2003; Palma & Figueroa 2008; Fochetti & Tierno de Figueroa 2008). Regional and local species diversities are less certain. Some tropical genera e.g. *Anacroneturia* are species-rich (Stark 2001) and few local surveys are available. Here we describe the stonefly fauna of a catchment in

the Wet Tropics Area of northeastern Australia.

Stream research in the Wet Tropics region (Pearson 1994) began as faunistic (Pearson et al. 1986) and process investigations at single localities and has expanded to include comparative, geographically extensive analyses (McKie et al. 2005; Pearson 2005; Connolly et al. 2008). Our intermediate scale project sampled multiple sites along gradients of elevation and stream size within a single catchment. Much stream research e.g. Cheshire et al. (2005) emphasizes functional roles of immature insects typically identified to family or genus. In contrast, we collected adults which can be identified reliably to the species level. In a potentially diverse and incompletely known tropical fauna, this was

important. The tradeoff, of course, is number of specimens; less numerous adults are less likely to be collected at all sites where larvae occur. We describe occurrence patterns over space and time and statistically evaluate the effect of limited collection size on interpretation. This problem may be especially acute in tropical streams so we suggest tactics to improve surveys such as ours.

## MATERIAL AND METHODS

Running River originates as Birthday Creek and flows westward to the Burdekin River from the coastal ranges of northern Queensland near the village of Paluma (19° 00' S, 146° 12' E), 70 km north of Townsville. The catchment lies in Mount Spec State Forest. Human impacts include limited logging, past tin mining, a few roads and a water supply reservoir on a tributary. Highest point in the drainage is 1020 m. Bedrock is granite and soils are shallow and nutrient poor (Congdon and Herbohn 1993). Rainforest at higher elevations grades downward to sclerophyll woodland at our lowest site (640 m). Small rainforest streams are densely shaded, becoming more open with increasing size and entry into woodland. Stream profiles are stepped with lower gradient reaches alternating with steeper sections and waterfalls. Water at higher elevations is weakly acidic (pH 6.2-6.5) and soft (conductivity 32 $\mu$ S/cm) (Pearson & Connolly 2000). Climate is wet but seasonal (Frith & Frith 1985) with a cool, dry winter (June-August) and a warm, wet summer (December-March). Stream flow reflects the seasonal rainfall but varies considerably between years. Our study began late in a three year drought but included a cyclonic rain January 31-February 1 1994 (948 mm at Paluma weather station). This storm scoured the streams but much less severely than did a 1991 cyclone (R. G. Pearson, pers. comm.). Stream temperatures 1993-1994 in Birthday Creek (785 m) ranged from monthly minima of 9-11°C (July, August) to maxima of 21°C (Nov.-Feb.) (Z. Rosser, pers. comm.).

We collected adult insects using battery-powered Rothamsted light traps with 12V fluorescent bulbs (Williams 1948; Benson & Pearson 1988) at 24 sites. The project was done within the confines of an academic leave; collections began 15 October 1993 and terminated 8 July 1994. The missing months are times of low insect activity (Frith & Frith 1985;

Benson & Pearson 1988) but our description of seasonal patterns is incomplete. We began with regular sampling of two small rainforest streams (Birthday Creek, 820 m; un-named tributary of Camp Creek, 760 m) as part of life history studies. By late November an array of sites, 640-940 m elevation on small to large streams, was in place (n=24). The two primary sites were sampled during each 2-4 d collecting bout (n=22). The remaining sites were sampled 1-8 times. Difficult access to some sites, equipment failures and others' need for the equipment kept the design from being balanced but the 130 successful collections (overnight operation, substantial insect catch) on 45 nights were fairly evenly distributed over time (12-18 collections per month), elevation and stream size. Larvae were collected with a kickscreen at the two primary sites October-April and at most other sites in October; these incomplete data are briefly mentioned in this paper.

Each site was described by two variables, elevation and stream size, derived from 1:50,000 topographic maps and general notes were made on channel form, riparian vegetation and canopy closure. Stream size was indexed by link magnitude (Shreve 1966) which is the total number of first order tributaries to a stream segment. The downstream site on Running River is order 5, magnitude 285 and 12 stream km from the source of Birthday Creek. Sheldon (1985) used elevation and magnitude to summarize stonefly distributions in a North American drainage. Some correlation of elevation and magnitude is inevitable since the largest stream in a drainage network occurs at the lowest elevation, but the correlation ( $r = -0.75$ ) is especially strong here because small, low elevation tributaries were dry most of the time and were not sampled. However, all mapped streams were counted in link magnitudes.

Taxonomic nomenclature follows Michaelis and Yule (1988) and McLellan (1996). Collections are deposited at James Cook University (Townsville) and the Australian National Insect Collection (Canberra).

Results are presented in descriptive graphics. However, given the variable collecting effort and the small number of stoneflies collected, we applied statistical procedures to evaluate the strength and generality of our results. For example, how successful were we in achieving a reasonably complete species list? To answer this question,

following guidelines in Brose et al. (2003), we used the first order jackknife estimator and its variance (Heltshe & Forrester 1983):

$$S_{est} = S_{obs} + (1 - 1/C) S_1$$

where  $S_{est}$  is the estimated total number of species,  $S_{obs}$  the number of species actually collected,  $C$  the number of collection units, and  $S_1$  the number of singleton species each collected in a single unit. The jackknife is a bias correction; an intuitive explanation for increasing  $S_{obs}$  by  $S_1$  is that each species collected just once likely had an uncollected counterpart.

We used multiple regressions, both linear and polynomial, to evaluate patterns of species richness over time and the gradient of elevation and stream size (log magnitude). Collection number, as log  $C$ , by month or site was included as a covariate in all regressions. For correlation and regression analyses we followed Sokal & Rohlf (1981), Zar (1984) and routines in SYSTAT 10.2 (SYSTAT 2002).

Diversity (species richness) is but one measure of

community structure. To assess compositional patterns over time and space we used Canonical Correspondence Analysis (CCA) executed in PC-ORD 4 (McCune & Mefford 1999). CCA is a multivariate constrained ordination technique which identifies the maximal correlation(s) between the matrix of species occurrences or abundances and the corresponding matrix of environmental variables. The regression model incorporated in CCA accommodates unimodal responses to environmental factors. For the temporal analysis we used frequencies of species occurrences ((trap nights/species/month)/(total trap nights/month)) with time (month) and collection number (log  $C$ ) in the biological and environmental matrices respectively. Occurrence (presence vs. absence) at sites and elevation, stream size (log magnitude) and collections/site (log  $C$ ) were used in the spatial analysis. Species occurring just once were omitted from CCA and June (no stoneflies) and July were combined in the temporal CCA. Statistical significance was set at  $P = 0.05$  for all analyses.

**Table 1. Composition and abundance of stoneflies in light trap catches from Running River.**

	Individuals	Collections	Sites
<b>Eustheniidae</b>			
<i>Cosmioperla wongoonoo tropica</i> (Theischinger)	8	6	2
<b>Gripopterygidae</b>			
<i>Dinotoperla cardaleae</i> Theischinger	291	41	17
<i>Illiesoperla barbara</i> Theischinger	18	10	8
<i>Illiesoperla cerberus</i> Theischinger	4	4	4
<i>Illiesoperla franzeni</i> (Perkins)	14	4	2
<i>Kirrama abolos</i> Theischinger	1	1	1
<i>Leptoperla alata</i> Theischinger	4	4	2
<i>Leptoperla commoni</i> Theischinger	5	3	3

## RESULTS

Stoneflies were neither abundant nor diverse in light trap catches from the Running River drainage (Table 1). Of the 130 collections, only 55 (42%) contained stoneflies from 19 sites (79%). The eight species collected were dominated by *Dinotoperla cardaleae* constituting 84% of the 345 stoneflies collected and found at 89% of occupied sites. In

contrast, a single *Kirrama abolos* was collected. The remaining species, although few in numbers, were captured in multiple collections at multiple sites. Applying the jackknife estimator to the occurrence by collection (trap night) (Table 1) yields  $S_{est} = 8.98$  with 95% confidence limits (8.00, 10.94) indicating that few or no additional species remained undetected.

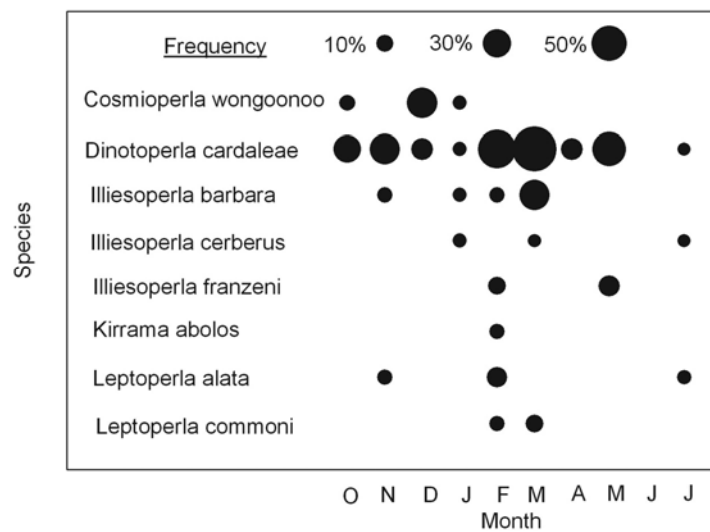


Fig. 1. Seasonal occurrence by months of Running River stoneflies in light traps. Frequency = (traps occupied/total traps per month) x 100.

Flight periods were prolonged (Fig. 1). Adults, including those of the abundant *D. cardaleae*, were collected October-July. However, some seasonality was suggested. The onset of cool, dry weather in April reduced captures and no stoneflies were captured in June. Stonefly diversity peaked January-March. Single species also showed some evidence of seasonality. *Cosmioperla wongoonoo* emerged toward the end of the dry season and

larvae with darkened wing pads were not taken after January although Theischinger (1983) recorded adults, from various locations, most months of the year. The frequency of occurrence of *D. cardaleae* peaked February-March and numbers increased also; the six largest collections all occurred in March. The high flows generated by Cyclone Sadie Jan.31-Feb. 1 did not suppress subsequent stonefly captures.

**Table 2. Summary statistics for regressions of species richness (S) on time (t), elevation, stream magnitude and number of collections (C). Entries under variables are standard partial regression coefficients with probabilities in ( ).**

Dependent	t	t <sup>2</sup>	log C	adj R <sup>2</sup>
a) log (S+1)	-0.093	-0.419	0.820	0.706
P	(0.900)	(0.600)	(0.001)	(0.015)
	elevation	log magnitude	log C	adj R <sup>2</sup>
b) log (S+1)	0.358	0.314	0.868	0.527
P	(0.190)	(0.205)	(0.001)	(0.001)

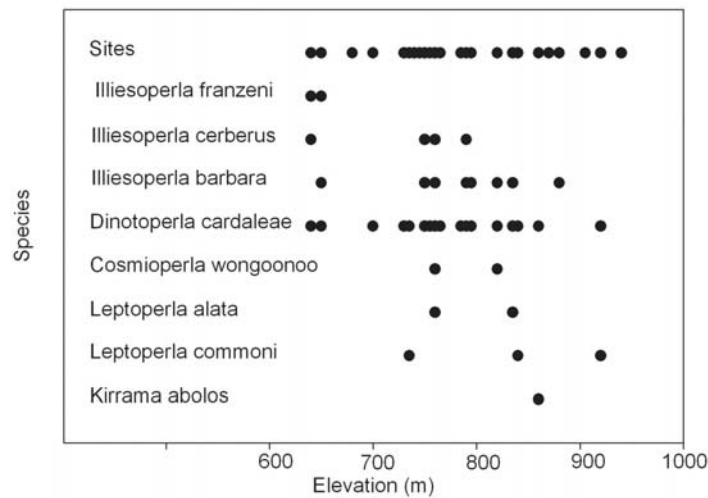


Fig. 2. Occurrence of Running River stoneflies at 24 sites over the elevation gradient. Species names are sequenced from those occurring at low elevation to those found in higher streams.

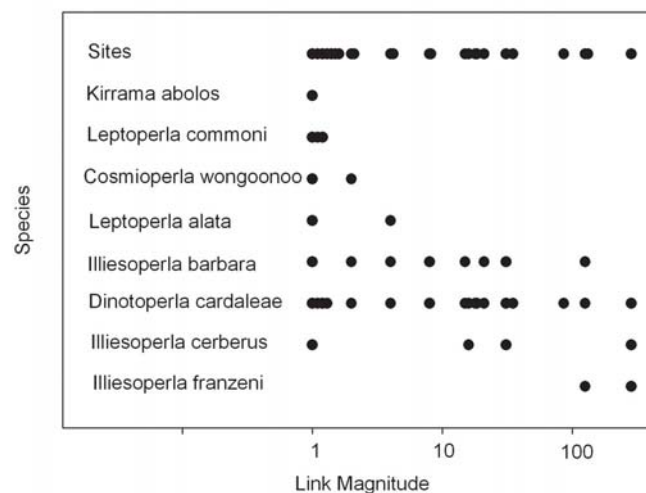


Fig. 3. Occurrences of Running River stoneflies over the gradient of stream size where magnitude 1 streams are the smallest. Species names are sequenced from those occurring in small streams to those found in large streams. Overlapping points have been displaced slightly for clarity.

We present spatial patterns relative to both elevation and stream magnitude (Fig. 2, 3). Some species (*D. cardaleae*, *Illiesoperla barbara*) were broadly distributed along both gradients. One species (*Illiesoperla franzeni*) occurred in larger, lower streams but four species (*C. wongoonoo*, *Leptoperla* spp., *K. abolos*) characterized smaller, higher streams. Note that *Leptoperla commoni*, occupying 200 m of the

elevation gradient, was confined to small streams. Conversely, the three *Illiesoperla* spp. appeared more closely associated with elevation than stream size. Records were sparse for most species and additional collecting undoubtedly will extend and clarify habitat usage. For example, in October 1993 we made a special effort to locate populations of *C. wongoonoo* but found larvae only at the two sites

**Table 3. Summary statistics for canonical correspondence analysis (CCA) of a) species composition (frequency of occurrence relative to time and number of collections, and b) species composition (presence-absence) relative to elevation, stream magnitude and number of collections. Coefficients for species and environmental variables for (b) are shown in Fig. 4.**

a) Time			
	Axis 1	Axis 2	
Eigenvalue	0.187	0.128	
% variance	18.0	12.4	
P	0.508	0.056	
Spp-Envir correlation	0.688	0.807	
P	0.848	0.124	
b) Space			
	Axis 1	Axis 2	Axis 3
Eigenvalue	0.434	0.291	0.099
% variance	23.2	15.6	5.3
P	0.006	0.002	0.012
Spp-Envir correlation	0.851	0.899	0.554
P	0.046	0.002	0.084

where adults were collected and in a larger stream (magnitude 22, elevation 785 m), thus supporting the elevation preference but extending the range of stream size for this species.

We tested the diversity pattern suggested in Fig. 1 by regressing  $\log(S+1)$  on  $t$ ,  $t^2$  and  $\log C$ . The full polynomial model (Table 2) was significant ( $P=0.015$ , adjusted  $R^2=0.71$ ) but only  $\log C$  contributed significantly. Thus the apparent diversity peak in January to March was not supported. The CCA of species composition (Fig. 1) leads to a similar conclusion (Table 3). Both  $t$  and  $\log C$  contributed to both canonical axes but only the second axis approached significance and neither of the species-environment correlations was significant. Seasonal succession suggested by Fig. 1 was not supported. The power of these analyses is low since data were grouped into just ten monthly periods.

To examine spatial trends in richness (0-5 spp./site) over all 24 sites we regressed  $\log(S+1)$  on elevation,  $\log$  magnitude and  $\log C$ . The full model (adjusted  $R^2=0.53$ ) was significant ( $P=0.001$ ) (Table 2) but only  $\log C$  contributed significantly ( $P=0.001$ ). Thus there were no detectable trends in species

richness over the gradient of elevation and stream size. Only collecting effort mattered. Note that this result was strongly influenced by the five sites without stoneflies and few collections (median  $C=1$ ).

Unlike richness, species composition varied along the elevation-stream size gradient although number of collections remained a confounding factor (Table 3, Fig.4). The primary gradient in Fig. 4 is elevation-stream size and the contribution of  $\log C$  comes primarily from the occurrence, probably fortuitous, of *C. wongoonoo* at the two primary sites selected for intensive sampling. All three canonical axes were significant and axes 1 and 2 represented significant species-environment correlations. Thus the broad patterns described in Fig. 2 and Fig. 3 were supported.

## DISCUSSION

The stoneflies of Running River included only two of four families of Australian stoneflies; Austroperlidae and Notonemouridae are restricted to temperate Australia (Michaelis & Yule 1988). The observed richness of eight species seems low to workers familiar with more diverse regional and



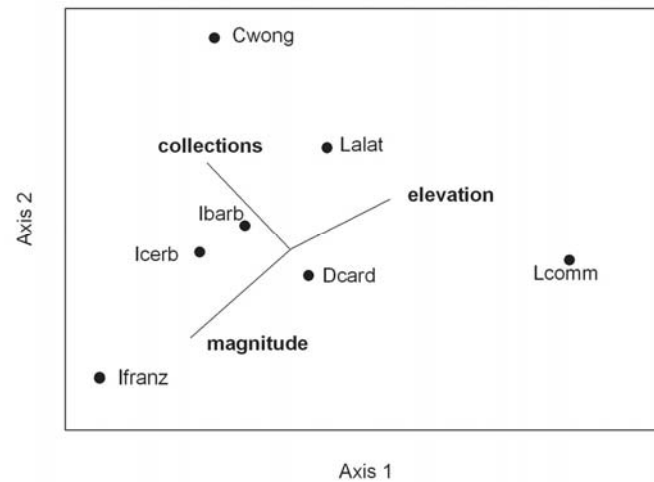


Fig. 4. Biplot of Canonical Correspondence Analysis (CCA). Points are species with abbreviations derived from names in Table 1. Lines show direction and relative importance (length) of environmental factors and collecting effort per site in the two-dimensional space jointly defined by species occurrences and gradients of elevation, stream size and collecting effort.

local faunas. However, Australia has only about 190 species of which 29 are known from north Queensland (Michaelis & Yule 1988; Theischinger 1988, 1991, 1993). Our jackknife extrapolation, with 95% confidence interval of 8-11 species, suggests that few species were missed. Similarly, Pearson et al. (1986) reported eight stonefly species from a well-studied single site on Yuccabine Creek 100 km north from our location and Monteith & Davies (1990) also found eight species at multiple sites along a transect in the Bellenden Kerr Range. In contrast, in temperate Australia Hynes & Hynes (1975) obtained 12-20 species at nine sites thoroughly sampled for larvae plus adults and accumulated 30 species across all sites. Available information is in accord with low tropical diversity of Plecoptera (Zwick 2000; Palma & Figueroa 2008; Fochetti & Tierno de Figueroa 2008) and differs from the conclusion of Lake et al. (1994) that the total invertebrate fauna of Birthday Creek was much more diverse than that of streams in temperate Australia.

Flight periods (Fig. 1) were extended and, at most, weakly seasonal. Similar lengthy emergence of stoneflies occurs in Brazil (Froehlich 1991) and weak seasonality persists near the equator (Zwick 1976). Coffman & de la Rosa (1998) compared emergence of chironomid Diptera in Costa Rica and Pennsylvania,

U.S.A.; emergence periods were 50-60% longer in the tropical assemblages. Emergence of Australian species tends to be protracted (Hynes & Hynes 1975; see Yule 1985 and Lake et al. 1985 for exceptions and discussion) and emergence of Running River stoneflies was fairly similar to congeners at 37° S.

Our study has significant limitations, especially the lack of collections from mid-July to October. Stoneflies are a cool-adapted group (Hynes 1976; Michaelis & Yule 1988) and additional species may have emerged in winter as they do in temperate regions. However, emergence would have to be unusually synchronous not to extend into the sampled months. The lack of collections from temporary streams at lower elevations is important because stoneflies tolerate such conditions (Yule 1985).

Light traps may not attract all the species present. However, adult aquatic insects in the tropics are mostly crepuscular or nocturnal (Edmunds & Edmunds 1980) and should be vulnerable to light traps. Ernst & Stewart (1985) light-trapped 11 of 12 stoneflies present in summer at a site in central U.S.A. and one of us has trapped many (sometimes 100s) of North American stoneflies difficult to collect by other means. However, independent methods (beating, searching, emergence trapping) could be

used concurrently to validate light trapping, especially in the cooler months. If flight activity is temperature dependent (Briers et al. 2003), then small cool season catches, which also occur in caddisflies (Benson & Pearson 1988) and terrestrial insects (Frith & Frith 1985) in this region, may be misleading. However, Frith & Frith (1985) attributed seasonality of insect catches to plant phenology as the proximate factor. Benson & Pearson (1988) considered seasonal patterns to be driven by larval life histories rather than adult behavior and vulnerability. Life history of a caddis species in Birthday Creek (Nolen & Pearson 1992) supports this view; cool season larvae were mostly early instars but late instar larvae, pupae and emergent adults were concentrated in the warmer months.

Spatial patterns relative to elevation and stream size (Fig. 2, 3) were consistent with broader zoogeographic patterns. Six species are part of a tropical montane fauna extending northward from the vicinity of Paluma through northeastern Queensland. Some of these species were confined to higher, smaller streams but others were more generalized. Two species are distributed primarily in southeastern Australia. *I. franzeni* seems to be part of an older eastern Australian fauna of larger, lower streams which matches its observed distribution in Running River. (This is the first record of *I. franzeni* north of the 350 km Paluma-Eungella gap, a significant faunal discontinuity for several taxa of aquatic insects (Watson & Theischinger 1984; Theischinger 2001)). *C. wongoonoo* is also part of this southeastern fauna but montane and, in Running River, was associated with tropical northern species in higher rainforest streams. These rainforest stoneflies may be vulnerable if a warming climate displaces habitat and populations upward into the limited and fragmented highlands of the Wet Tropics Region (Williams et al. 2003; Wilson et al. 2007).

Statistical support for our conclusions was diminished as a consequence of our opportunistic design and our decision to sample more sites but less intensively. Prior to our work, stoneflies had been collected only from a few easily accessible sites in the drainage. We elected to explore a wider range of habitats but at considerable cost in replication per site. Improved designs, based on the results of this survey, are suggested below.

A more general problem is that we captured few

adult stoneflies. Overall, our capture rate was 2.65 stoneflies/trap night. Similarly Zwick (1976) reported 988 Perlidae from a 9 m<sup>2</sup> emergence trap checked daily for 16 months in an African stream; i.e. 2.05 stoneflies/trap night. In addition, a single species dominated our collections (84%) and Zwick's (1976) emergence data (91%); the remaining species were uncommon. Recent experience of one author (ALS) in Bornean streams using beating sheet, light traps and kick net larval sampling supports the view that tropical stoneflies are scarce.

Our initial objective, taxonomic resolution, was attainable only by collecting adults which are the last few survivors of a larval cohort. Asynchronous emergence will further reduce daily catches, perhaps to the point of non-detection at a specific place or time. However, protracted emergence will increase the odds that a species will be detected somewhere at some time which seems to be the case in our data since the species list approached completeness. The consequences of rarity are variable data with many random absences and strong confounding of ecological effects with effort (number of collections) as implied by all our statistical analyses. The only solution is increased effort applied approximately equally at all sites and times.

A possible design for future work in Running River or other Wet Tropics streams would use fewer sites, perhaps 8-10, distributed over the gradients of stream size and elevation. Increased frequency of sampling (2-4 times per month) would increase total catch, refine temporal coverage and serve as insurance against periods of cyclonic rain and other unpredictable events. An appealing possibility is to use multiple traps (3-5), spaced far enough apart to avoid gear interference, at each site and time. This procedure also would increase total catch and allow explicit calculation of detection probabilities. This level of effort appears extreme. However, extrapolating from our catch rates and species proportions, a design of 8 sites, 4 traps/site and weekly sampling would yield 4410 stoneflies of which only 705 would be the seven non-*Dinotoperla* species with catches ranging 13-233 individuals (median=59). This level of effort might also detect one or more of the additional species predicted by the jackknife estimate. Alternative collecting methods (beating sheet, emergence traps, Malaise traps) should be used to determine bias and efficiency of



light trapping. With this level of investment, and made possible by our species list and other data, larval sampling for life-history and population studies would be warranted although the number of sites might have to be reduced.

In conclusion, across multiple sites in a single tropical catchment, adult stoneflies were numerically rare, of low diversity, weakly seasonal and showed moderate habitat specialization for elevation and stream size. Tropical stonefly assemblages require substantial sampling effort to obtain ecological data on any but the dominant species.

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#### REFERENCES

Benson, L.J. & R.G. Pearson. 1988. Diversity and seasonality of adult Trichoptera captured in a light-trap at Yuccabine Creek, a tropical Australian rainforest stream. *Australian Journal of Ecology*, 13:337-344.

Bispo, P.C. & L.G. Oliveira. 2007. Diversity and structure of Ephemeroptera, Plecoptera and Trichoptera (Insecta) assemblages from riffles in mountain streams of Central Brazil. *Revista Brasileira de Zoologia*, 24:283-293.

Briers, R., A., H.M. Cariss, & J.H.R. Gee. 2003. Flight activity of adult stoneflies in relation to weather. *Ecological Entomology*, 28:31-40.

Brose, U., N.D. Martinez, & R.J. Williams. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, 84:2364-2377.

Cheshire, K.L., L. Boyero, & R.G. Pearson. 2005. Food

webs in tropical Australian streams: shredders are not scarce. *Freshwater Biology*, 50:748-769.

Coffman, W.P. & C.L. de la Rosa. 1998. Taxonomic composition and temporal organization of tropical and temperate species assemblages of lotic Chironomidae. *Journal of the Kansas Entomological Society*, 71:388-406.

Congdon, R.A. & J.L. Herbohn. 1993. Ecosystem dynamics of disturbed and undisturbed sites in north Queensland wet tropical rain forest. I. Floristic composition, climate and soil chemistry. *Journal of Tropical Ecology*, 9:349-363.

Connolly, N.M., F. Christidis, B. McKie, L. Boyero, & R. Pearson. 2008. Diversity of invertebrates in Wet Tropics streams: patterns and processes. Pages 161-177. *In* N. Stork (editor). *Living in a Dynamic Tropical Landscape*. Blackwell Publishing, London.

Edmunds, G.F. & C.H. Edmunds. 1980. Predation, climate and mating in mayflies. Pages 277-286. *In* J.F. Flannagan & K.E. Marshall (editors). *Advances in Ephemeroptera Biology*. Plenum Press, New York, New York, U.S.A.

Ernst, M.R. & K.W. Stewart. 1985. Emergence patterns and an assessment of collecting methods for adult stoneflies (Plecoptera) in an Ozark foothills stream. *Canadian Journal of Zoology*, 63:2962-2968.

Fochetti, R. & J.M. Tierno de Figueroa. 2008. Global diversity of stoneflies (Plecoptera: Insecta) in freshwater. *Hydrobiologia*, 595:365-377.

Frith, C.B. & D.W. Frith. 1985. Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology*, 10:237-248.

Froehlich, C.G. 1991. Flight periods of *Kempnyia* and *Macrogynoplax* (Plecoptera: Perlidae) in southeastern Brazil. Pages 353-357. *In* J. Alba-Tercedor & A. Sanchez-Ortega (editors). *Overview and strategies of Ephemeroptera and Plecoptera*. Sandhill Press, Inc., Gainesville, Florida, U.S.A.

Heltshe, J.F. & N.E. Forrester. 1983. Estimating species richness using the jackknife procedure. *Biometrics*, 39:1-11.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist*, 163:192-211.

Hynes, H.B.N. 1976. *Biology of Plecoptera*. Annual

- Review of Entomology, 21:135-153.
- Hynes, H.B.N. & M.E. Hynes. 1975. The life histories of many of the stoneflies (Plecoptera) of south-eastern mainland Australia. *Australian Journal of Marine and Freshwater Research*, 26:113-153.
- Lake, P.S., L.A. Barmuta, A.C. Boulton, I.C. Campbell & R.M. St. Clair. 1985. Australian streams and Northern Hemisphere stream ecology: comparisons and problems. *Proceedings Ecological Society of Australia*, 14:61-82.
- Lake, P.S., E.S.G. Schreiber, B.J. Milne, & R.G. Pearson. 1994. Species richness in streams: patterns over time, with stream size and with latitude. *Verhandlungen Internationale Vereinigung Limnologie*, 25:1822-1826.
- McKie, B.G., R.G. Pearson, & P.S. Cranston. 2005. Does biogeographical history matter? Diversity and distribution of lotic midges (Diptera: Chironomidae) in the Australian Wet Tropics. *Austral Ecology*, 30:1-13.
- McLellan, I.D. 1996. A revision of *Stenoperla* (Plecoptera: Eustheniidae) and removal of the Australian species to *Cosmioperla* new genus. *New Zealand Journal of Zoology*, 23:165-182.
- McCune, B. & M.J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach, Oregon, U.S.A.
- Michaelis, F.B. & C.M. Yule. 1988. Plecoptera. *Zoological Catalog of Australia*, 6:133-176.
- Monteith, G.B. & V.T. Davies. 1990. Preliminary account of a survey of arthropods (insects and spiders) along an altitudinal rainforest transect in tropical Queensland. Pages 345-413. *In* G. Werren & P. Kershaw (editors). *The rainforest legacy*, Vol. 2, Flora and fauna of the rainforests. Australian Heritage Commission, Special Publication no. 7. Australian Government Publishing Service, Canberra.
- Nolen, J.A. & R. G. Pearson. 1992. Life history studies of *Anisocentropus kirramus* Neboiss (Trichoptera: Calamoceratidae) in a tropical Australian rainforest stream. *Aquatic Insects*, 14:213-221.
- Palma, A. & R. Figueroa. 2008. Latitudinal diversity of Plecoptera (Insecta) on local and global scales. *Illiesia*, 4:81-90.
- Pearson, R.G. 1994. Limnology in the northeastern tropics of Australia, the wettest part of the driest continent. *Mitteilung Internationale Vereinigung Limnologie*, 24:155-164.
- Pearson, R.G. 2005. Biodiversity of the freshwater invertebrates of the Wet Tropics region of northeastern Australia: patterns and possible determinants. Pages 470-485. *In* E. Bermingham, C. W. Dick & C. Moritz (editors). *Tropical rainforests: past, present and future*. University of Chicago Press, Chicago, Illinois.
- Pearson, R.G., L.J. Benson, & R.E.W. Smith. 1986. Diversity and abundance of the fauna of Yuccabine Creek, a tropical rainforest stream. Pages 329-342. *In* P. DeDekker & W.D. Williams (editors). *Limnology in Australia*. CSIRO and Junk, Melbourne, Victoria.
- Pearson, R.G. & N.M. Connolly. 2000. Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology*, 43:31-42.
- Sheldon, A.L. 1985. Perlid stoneflies (Plecoptera) in an Appalachian drainage: a multivariate approach to mapping stream communities. *American Midland Naturalist*, 113:334-342.
- Shreve, R.L. 1966. Statistical law of stream numbers. *Journal of Geology*, 74:17-37.
- Sokal, R.R. & F.J. Rohlf. 1981. *Biometry*. W.H. Freeman & Company, New York.
- Stark, B.P. 2001. A synopsis of the Neotropical Perlidae. Pages 405-422. *In* E. Dominguez (editor). *Trends in Research in Ephemeroptera and Plecoptera*, Kluwer Academic/ Plenum Publishers, New York.
- SYSTAT. 2002. SYSTAT 10.2. SYSTAT Software Inc., Richmond, California.
- Theischinger, G. 1983. The genus *Stenoperla* McLachlan in Australia (Insecta: Plecoptera: Eustheniidae). *Australian Journal of Zoology*, 31:541-556.
- Theischinger, G. 1988. New and little known species of stoneflies from Australia (Insecta: Plecoptera). *Stapfia*, 17:147-157.
- Theischinger, G. 1991. Plecoptera (Stoneflies). Pages 311-319. *In* I.D. Naumann et al. (Editors). *Insects of Australia. A textbook for students and research workers*. Second edition. Vol. I. Melbourne University Press.
- Theischinger, G. 1993. New species of Australian stoneflies (Insecta: Plecoptera). *Linzer biologische Beiträge* 25:821-832.
- Theischinger, G. 2001. Regions of taxonomic

- disjunction in Australian Odonata and other freshwater insects: second addendum with the description of *Austroaeschna unicornis pinheyi* ssp. nov. (Anisoptera: Aeshnidae). *Odonatologica*, 30:87-96.
- Vinson, M.R. & C.P. Hawkins. 2003. Broad-scale geographical patterns in local stream insect genera richness. *Ecography*, 26:751-767.
- Watson, J.A.L. & G. Theischinger. 1984. Regions of taxonomic disjunction in Australian Odonata and other freshwater insects. *Odonatologica*, 13:147-157.
- Williams, C.B. 1948. The Rothamsted light trap. *Proceedings of the Royal Entomological Society of London*, 23:80-85.
- Williams, S.E., E.E. Bolitho, & S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings Royal Society London B*, 207:1887-1892.
- Wilson, R.D., J.W.H. Trueman, S.E. Williams, & D.K. Yeates. 2007. Altitudinally restricted communities of Schizophoran flies in Queensland's Wet Tropics: vulnerability to climate change. *Biodiversity and Conservation*, 16:3163-3177.
- Yule, C. 1985. Comparative study of the life cycles of six species of *Dinotoperla* (Plecoptera: Gripopterygidae) in Victoria. *Australian Journal of Marine and Freshwater Research*, 36:717-735.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall Inc., Englewood, New Jersey.
- Zwick, P. 1976. *Neoperla* (Plecoptera: Perlidae) emerging from a mountain stream in central Africa. *Internationale Revue Gesamten Hydrobiologie*, 61:683-697.
- Zwick, P. 2000. Phylogenetic system and zoogeography of the Plecoptera. *Annual Review of Entomology*, 45:709-746.

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