Article

Dynamics of Invertebrate Diversity in a Tropical Stream

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Abstract: Regional studies of biotic communities are important for characterising their normal spatial and temporal variation, but there are few such studies of tropical streams. This paper describes changes in invertebrate communities in Yuccabine Creek, a seasonal upland rainforest stream in tropical Australia, over three-year and decadal periods. Invertebrate abundance, richness and evenness were temporally stable, except after major drying or wet-season flows, from which they recovered quickly; however, three wet seasons contrasted in abundance patterns. Species' responses to flood or drought varied depending on life-histories and habitat dynamics. Communities showed contrasts between wet, early-dry and late-dry seasons, with different characteristic species. Current velocity, leaf litter and substratum particle size were the main environmental correlates with species abundances and multivariate scores. Between-decade contrasts were due to antecedent rainfall and loss of canopy cover. Trophic composition varied seasonally, driven by abundances of predators and detritivores. Yuccabine Creek differs from comparable temperate streams in its high diversity of invertebrates, continual recruitment and spring-dominated continual leaf fall; and from some other tropical streams in its seasonal flow regime. Interpretation of invertebrate metrics in these streams needs to account for historical, antecedent and current conditions, but biannual samples would adequately characterise the fauna.

1. Introduction

Understanding the diversity of assemblages requires information on both spatial and temporal variation as species composition and attendant community properties can be patchy and cyclical. For example, stream invertebrate assemblages can be patchy even within single riffles [1–3] and show strong responses to temporal changes in environmental variables such as flow [4,5]. Consequently, there may be distinct shifts not only in population sizes but also in composition and in functioning of food webs [6]. Therefore, although stream communities may be persistent in the long term [7–9], they can be variable in structure and composition according to seasonal and other environmental change. This means that community measures such as richness, evenness and abundance vary in space and time, so ecological studies, biodiversity assessments and monitoring programs need to be timed and located appropriately to properly represent the target communities.

Most descriptive studies of stream communities have been undertaken in temperate Europe and North America, although there is increasing interest in tropical systems across the globe [10]. There have been several considerations of differences between temperate and tropical systems [11,12], which might suggest substantial similarity within those zones. But just as there is great variability among temperate streams, some characteristics of tropical streams such as temperature regimes and flow predictability vary according to latitude, altitude, *etc*. In the tropics, streams range from intermittent in the seasonal wet/dry tropics [13,14] to daily flooded near the equator [15,16]. In wet tropical regions flow is usually perennial, but becomes more seasonally variable with distance from the equator, and subject to local weather patterns [17]. We might expect, therefore, that stream communities will reflect these differences.

Geographically widespread studies are required to characterise similarities and differences in comparable systems across the globe, but few studies are available that describe invertebrate dynamics of tropical streams over several years. This paper describes dynamics of invertebrate communities at a single site in an upland rainforest stream, Yuccabine Creek, in tropical Australia, over an initial three-year period in the 1980's, and subsequently about a decade later. This stream is seasonal but normally perennial, unlike streams across the majority of northern Australia [17,18]. It has a diverse invertebrate fauna with species variously breeding throughout the year or seasonally [19]. The study aimed to determine the main biophysical drivers (e.g., flow, substratum) of assemblage composition and structure (species' richness, evenness, presence/absence, abundance and trophic relationships) and whether these variables were consistent among small-scale patches and between months and years, including periods of flood and drought.

2. Methods

2.1. Site Description

Yuccabine Ck. is a headwater tributary of the Herbert River, in the Queensland Wet Tropics bioregion on the north-eastern coast of Australia [19]. The Wet Tropics comprises 18,497 km^2 (only 0.26% of Australia) of ancient weathered mountain ranges, steep streams and gorges and short floodplains, with eastern-flowing streams entering the Great Barrier Reef lagoon. The natural vegetation of the region is mainly tropical rainforest, merging into tall open forest and savannah woodlands to the west and mangroves towards the coast, but with tablelands and coastal floodplains cleared for agriculture. The

forested areas have been selectively logged in the past, including a short period during this study, but are now largely protected in national parks and the Wet Tropics World Heritage Area. Annual rainfall at Cardwell, 29 km from the study site, averages 2140 mm, with about 80% falling in the summer wet season (December–April) (data from the Australian Bureau of Meteorology).

Yuccabine Ck. rises at about 900 m elevation and flows south through montane rainforest. At the study site (18.205°S, 145.765°E, ~615 m elevation) it is a 3rd-order stream, about 5 m wide, with alternating riffles and pools. The bedrock is granite and the substratum comprises mainly granitic cobbles and rocks, interspersed with gravel, sand and leaf litter (Table 1). During the period of this study, current velocity at base flow ranged from 0 to 100 cm s^{-1} (measured using a Marsh-McBirney meter); water temperature ranged from 10.5 to 25 °C (measured with a max-min thermometer left in the stream); the water was well oxygenated (YSI meter), slightly acidic (YSI meter) and with low conductivity (Hach meter) and nutrient concentrations (water samples analysed using standard methods); like other Australian coastal streams, sodium and potassium were the dominant dissolved cations [20] (Table 1). Canopy cover over the stream averaged about 80% but was reduced to about 40% by severe tropical cyclone Winifred (1986) [21]. The stream had no gauging station but, on each visit, stream discharge was estimated by measuring cross-sectional area and current velocity at a culvert. Small-scale selective logging in the catchment (January 1982) had little observable effect on the stream, the condition of which was regarded as near-pristine.

Table 1. Biophysical descriptors of the Yuccabine Creek sampling site (from across all samples, in non-flood conditions). CPOM is coarse particulate organic matter (mainly leaf litter); FPOM, fine particulate organic matter; DO, dissolved oxygen. Periphyton and bryophytes were scored on a 0–5 scale, equivalent to % cover of 0, 1–20, 21–40, 41–80 and >80. Substrata are described by mean size or proportion of sample area in each category.

	Mean	**s.e.**	**Maximum**	**Minimum**
Periphyton (0–5 scale)	2.67	0.16	5	1
Bryophyte (0–5 scale)	0.70	0.16	3	0
Discharge (m$^3 \cdot$s^{-1})	0.217	0.038	0.70	0
Current (cm$\cdot$s^{-1})	27.08	1.72	100	0
Depth (cm)	12.17	0.93	25	6
% CPOM	9.50	1.09	20	0
% FPOM	7.19	0.97	20	0
% Gravel, φ ≥ −2	9.84	1.95	50	0
% Gravel, φ = −3	5.78	0.70	20	0
% Gravel, φ = −4	2.97	0.61	10	0
% Gravel, φ = −5	3.59	0.73	10	0
% Cobble, φ = −6	10.62	1.56	30	0
% Cobble, φ = −7	33.11	4.96	90	0
% Boulder, φ = −8	26.87	5.12	85	0
Mean substratum (φ)	−5.33	0.11	−8	−1
Temperature (°C)	18.93	2.46	25.1	10.5
Conductivity (μS/cm)	48.13	5.11	70.1	33.4
DO (% saturation)	80.50	2.02	85.1	77.5
pH	6.53	0.14	6.9	5.9

	Mean	**s.e.**	**Maximum**	**Minimum**
Total N ($\mu g \cdot L^{-1}$)	121.1	47.6	229	48.7
Nitrate N ($\mu g \cdot L^{-1}$)	17.6	3.28	25	12.5
Total P ($\mu g \cdot L^{-1}$)	3.57	1.10	6.1	2.2
Phosphate P ($\mu g \cdot L^{-1}$)	2.31	0.95	4.5	1.03
Sodium ($mg \cdot L^{-1}$)	6.91	0.62	8.33	5.02
Potassium ($mg \cdot L^{-1}$)	1.01	0.07	1.16	0.9
Calcium ($mg \cdot L^{-1}$)	0.78	0.27	1.38	0.36
Magnesium ($mg \cdot L^{-1}$)	0.76	0.33	1.53	0.35

2.2. Sampling

Sampling of invertebrates was undertaken to investigate faunal composition, temporal dynamics, trophic relationships and their major drivers. Samples were collected approximately monthly from October 1981 to June 1984 (26 sets of samples), to capture seasonal and inter-annual change, with further samples in 1993–1995 (3 sets) to investigate longer-term change. Between 9 and 20 samples were taken on each occasion, haphazardly, from the length of a riffle (~50 m), representing about 50% of the habitat at the site (the rest was mainly rocky pools). Samples were collected by disturbing a 25 × 25 cm area of substratum upstream of a triangular net (400-µm mesh). Individual cobbles and rocks were scrubbed in the mouth of the net to remove attached animals. The proportion of the sample area covered by leaf litter was estimated prior to taking the sample, and current velocity and maximum substratum size (using a φ-scale gauge) were recorded immediately afterwards. Samples were preserved in 70% ethanol then returned to the laboratory for sorting and identification. Individuals were identified to species, or equivalent operational taxonomic units, except that, after the first year's sampling, the Chironomidae were not identified beyond family; and 1993–1994 samples were identified to family only.

2.3. Data Analysis

Analyses were undertaken on species-level data (1981–1982), species-level data but with Chironomidae lumped (1981–1984) or on family data (1981–1994). Evenness and Chao2 estimates of richness, a rarefaction technique that compensates for different numbers of sample units [22], were calculated in PC-ORD© 6 [23]. Assemblage data were analysed using Bray-Curtis similarity, non-metric multidimensional scaling (NMDS) and Indicator Species analysis in PC-ORD. Three NMDS analyses of species data (log-transformed abundance, proportional abundance and presence-absence data) were compared to determine whether taxonomic composition or changes in relative abundance had separate outcomes. The first axes of the ordinations represented the largest component of the variance in each case, and were strongly correlated (log abundance *vs.* proportion, $r = 0.905$, $p < 0.0001$; log abundance *vs.* presence-absence, $r = 0.944$, $p < 0.0001$), so only the log-abundance analyses are presented. Excel© was used to calculate Pearson correlations between NMDS axis scores and antecedent rainfall, and coefficients of variation of abundance and richness. Statistix© 7 was used for one-way ANOVA and *t*-tests on raw richness data to compare pre- and post-drought samples, and for linear regression analyses

between environmental variables, species' abundances and NMDS axis scores. The difference between decadal groups of samples was tested using Multi-Response Permutation Procedures (MRPP) in PC-ORD.

To analyse trophic composition of the fauna, all taxa were assigned to one of four trophic classes: shredders, detritivorous collector-gatherers, grazer-scrapers, and predators, following dietary analyses of Wet Tropics stream invertebrates [6]; filterers were assigned to the collector-gatherer or predator groups as appropriate. Data were ordinated using NMDS and differences among *a priori* seasonal groups were tested using MRPP. Temporal groupings were made according to the four quarters of the year, avoiding the need to pre-assign seasons, given that they can vary in their timing. The four quarters were essentially equivalent to wet season (1), late wet/early dry season (2), mid dry season (3), and late dry/early wet season (4).

3. Results

Rainfall and stream flow were high and variable in the wet season, and steadily diminished through the dry season (Figure 1a). Unexpectedly, flow ceased in November 1981, but remnant pools remained until flow recommenced in February 1982. The riffle was devoid of surface water during this period, which was termed "drought" because the event was unusual. Rainfall for nearby Cardwell was not unusually low for the antecedent months (Table A1), so it is possible that such drying might occur frequently, in response to local weather conditions, although it was not observed at any other time during this study.

Invertebrate abundance, richness and evenness per sample, and total richness maintained stable levels except in response to major flow or drying events (Figure 1b–e), peaking in the late dry season of 1982 and wet season of 1984. Richness per sample closely tracked abundance, representing enhanced sampling of species at greater densities, especially with diminishing flow, but also including species not previously recorded. The species richness of Chironomidae, in particular, climbed as flow declined and invertebrate densities increased, in 1981–1982. Total species richness and Chao2 estimates (based on the cumulative total of all replicates) were less variable as they more closely reflected the species pool. Following the drought period, richness and abundance recovered to previous levels over approximately four months following resumption of flow and were stable until after the next wet season, although within-sample variability was greater post-drought (Table 2).

Monthly 95% confidence limits of richness encompassed the overall mean in 15 of 26 months; those that exceeded the limits were pre-drought (July–October 1982) and post-wet season (April–May 1982, March–April 1983 and February–May 1984), indicating greater patchiness. Evenness was generally high (>0.8) but declined prior to the drought, indicating increased dominance by a few species, despite increasing richness; it returned to pre-drought levels after the drought.

Trends in these variables broadly followed changes in discharge (Figure 1a). Apart from the broad band of richness of about 20–40 species per sample unit and 60–90 species per sample through many samples, the annual patterns of richness were dissimilar. Bray-Curtis similarity among samples was mostly moderate and consistent, both within months and between adjacent months (Figure 1f), but similarity between months was higher than within months, indicating patchiness across the riffle, and faunal persistence with time. Within-month similarity was marginally lower post-drought (50.0% ± 1.3% *vs.* 54.7% ± 1.3%; $F_{1,24} = 6.14$, $p = 0.0206$), reflecting greater patchiness, and between-month similarity was lower after the drought (68.4% ± 2.4% *vs.* 76.3% ± 1.2%; $F_{1,23} = 6.45$, $p = 0.018$). Similarity between

years was higher and quite consistent: 1981–1982 *vs.* 1982–1983, 75.5%; 1981–1982 *vs.* 1984–1984, 78.0%; and 1982–1983 *vs.* 1984–1984, 79.0%.

Figure 1. Monthly changes in rainfall, flow and invertebrate community metrics (± s.e. where appropriate) in Yuccabine Creek. Dotted vertical lines indicate January of each year. The break in the X axis indicates cessation of surface flow ("drought").
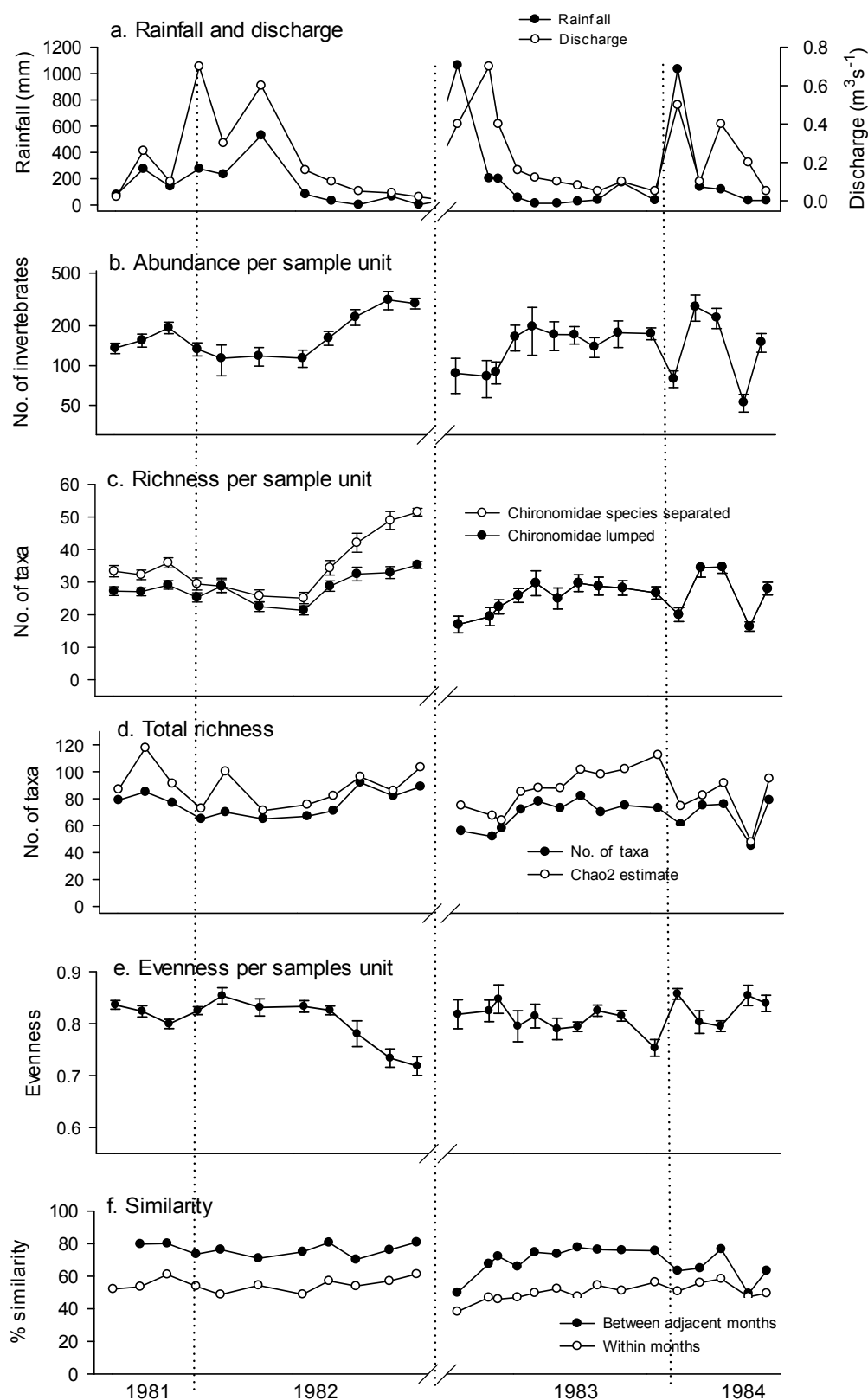
Table 2. Major differences (*t*-test, $p < 0.05$) in coefficient of variation (mean % ± s.e.) of invertebrate abundance and species richness five months (d.f. = 8) and 10 months (d.f. = 18) before and after drought.

	Pre-Drought		Post-Drought		*t*	*p*	Direction
Five months before and after drought							
Austrophlebioides sp.	209.5	±16.5	96.4	±11.8	5.60	0.001	−
Rhagovelia sp.	55.2	±4.8	9.5	±9.5	4.31	0.003	−
Tasmanocoenis sp.	99.2	±9.5	57.9	±4.6	3.92	0.004	−
Aeschnidae	115.8	±11.6	71.3	±5.6	3.47	0.008	−
Philorheithridae	85.9	±2.1	37.2	±15.3	3.17	0.013	−
Athericidae	128.0	±22.8	58.2	±15.8	2.52	0.036	−
Baetis sp.	128.4	±9.5	87.3	±13.3	2.52	0.036	−
Simuliidae	40.9	±2.7	74.7	±8.7	3.72	0.006	+
Illiesoperla sp.	53.2	±9.2	82.9	±6.4	2.66	0.029	+
Chimarra sp.	48.2	±5.5	66.8	±5.1	2.48	0.038	+
Species richness	22.1	±3.1	37.9	±4.1	3.07	0.015	+
Ten months before and after drought							
Philorheithridae	85.4	±2.3	48.6	±8.4	4.25	0.002	−
Austrophlebioides sp.	204.1	±14.2	130.3	±15.4	3.53	0.002	−
Cosmioperla sp.	94.0	±8.4	65.2	±6.2	2.75	0.014	−
Tasmanocoenis sp.	98.9	±5.5	75.5	±7.3	2.57	0.020	−
Anisocentropus sp.	54.7	±4.4	80.7	±7.4	3.02	0.009	+
Archicauliodes sp.	67.9	±4.5	86.8	±6.0	2.52	0.022	+
Simuliidae	48.5	±4.9	65.3	±5.8	2.23	0.039	+
Species richness	22.6	±1.7	33.2	±2.8	3.21	0.005	+

The more abundant taxa showed variable temporal patterns and responses to the drought and wet seasons (Figure 2). Some had stable abundances through all months, both before and after the drought (e.g., *Nousia* 2, *Atalomicria*, *Helicopsyche*, *Marilia*). Some increased in abundance post-drought (e.g., *Austrolimnius* 1, *Archicauliodes*), while others declined (e.g., *Tasmanocoenis*, Tipulidae, *Cheumatopsyche* A). For some, the post-drought recovery took several months (e.g., *Austrophlebioides*, *Baetis*) whereas for others, recovery had occurred by the time of the first post-drought sample. Some taxa increased in variability within months post-drought (e.g., *Simulium*, *Illiesoperla*) while others decreased (e.g., *Austrophlebioides*, *Rhagovelia*) (Table 2). Chironomidae as a whole showed high stability throughout, but this belied the different temporal patterns of individual species within a single year. Effects of the wet seasons on individual species' abundances were not great: some species, such as the filtering *Cheumatopsyche* species, increased post-wet season, some were very stable (e.g., the grazer *Helicopsyche*), while others declined but returned to pre-wet-season levels rapidly (e.g., the shredder *Anisocentropus* and the predator *Aeschna*). Decline in the wet season may be due to greater emergence at that time as well as disturbance [21].

Figure 2. Monthly changes in abundance (± s.e.) of the most numerous invertebrate taxa in Yuccabine Creek, October 1981–June 1984. Dotted vertical lines indicate January of each year.
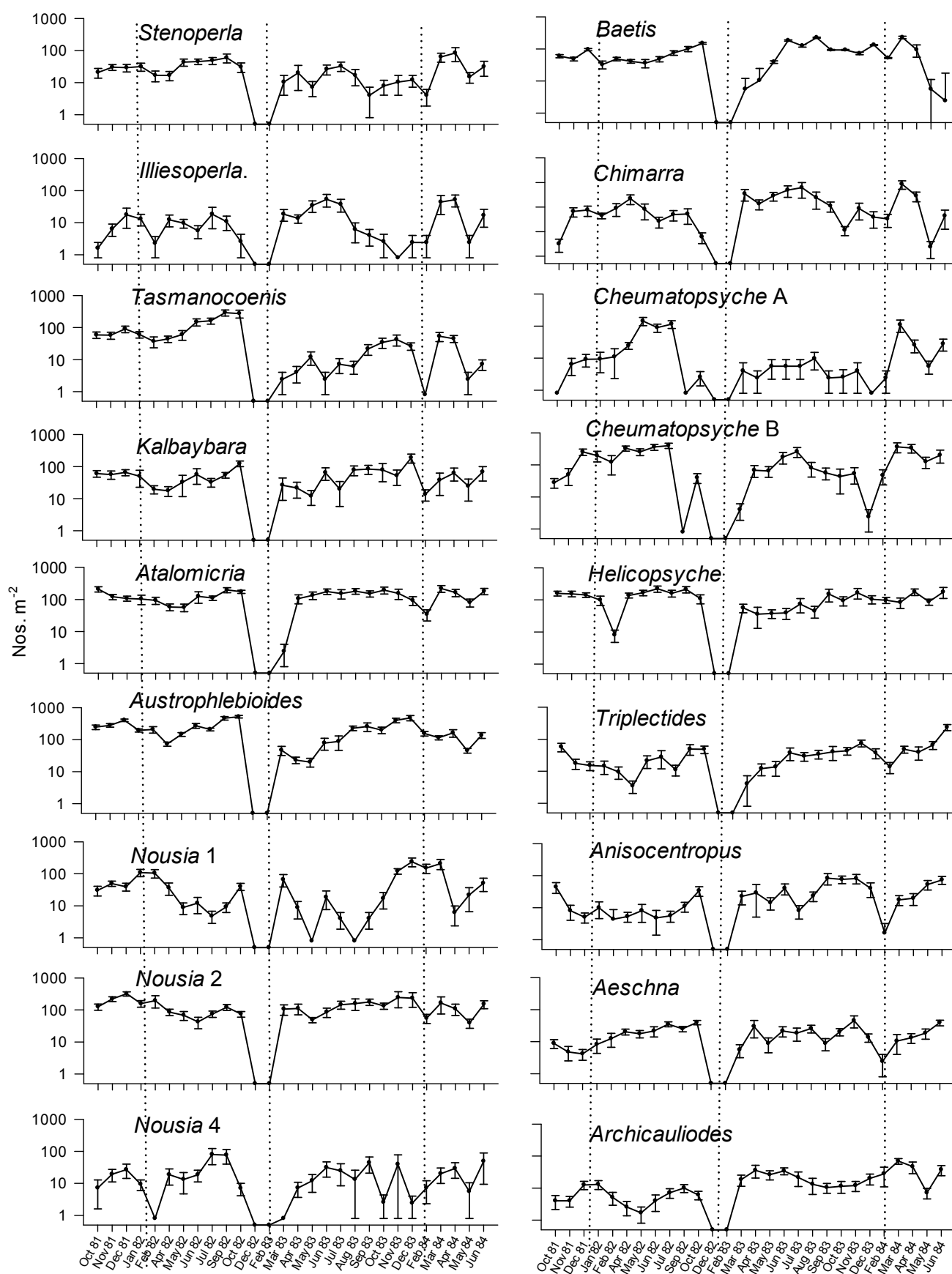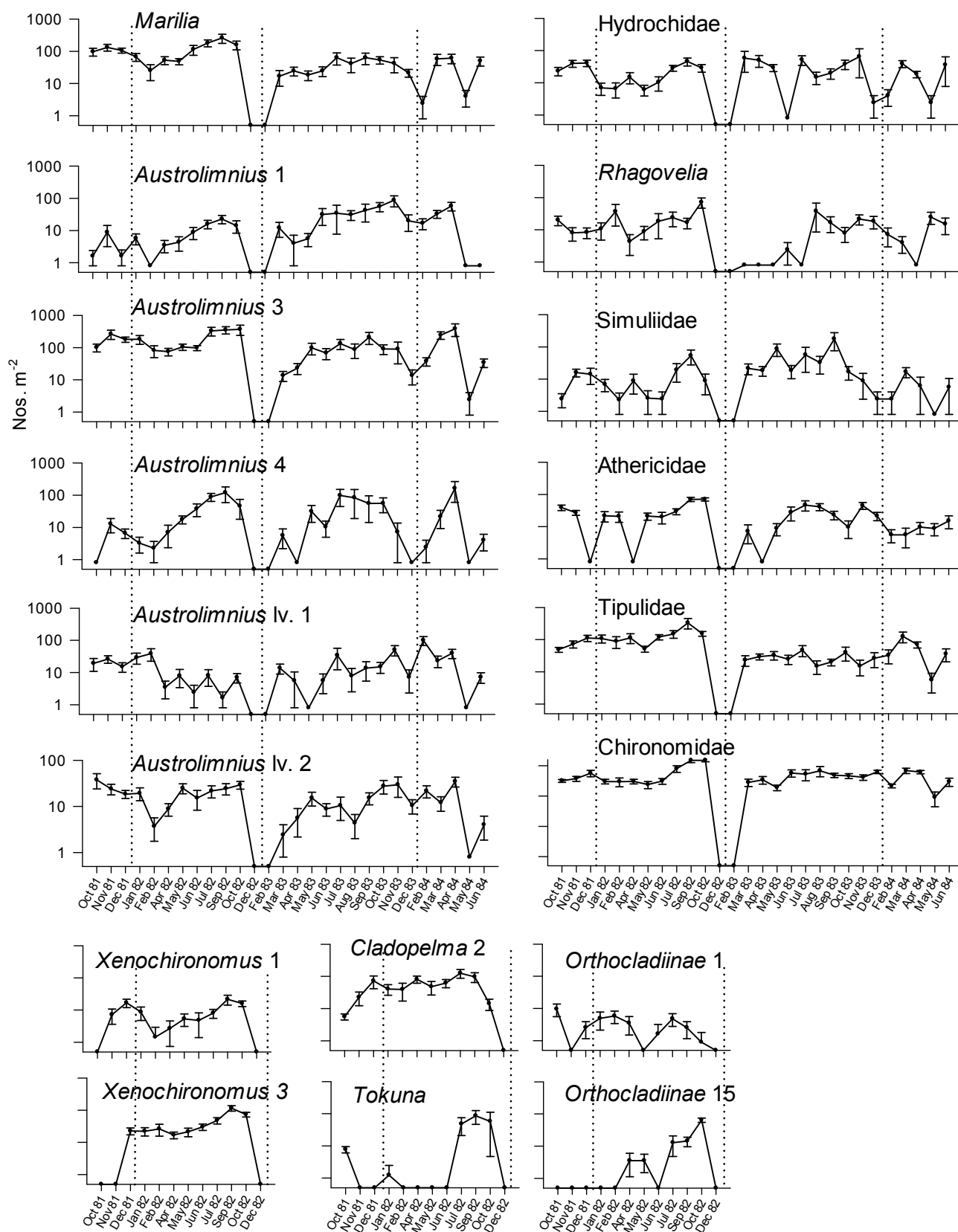
Figure 2. *Cont.*

The NMDS analysis of species data (other than Chironomidae) for 1981 to 1984 showed seasonal responses on the first two axes with the wet season separating from the dry season on axis 1, and the dry season being divided into early and late periods on axis 2 (Figure 3). Overlap between these seasons in

multivariate space may be less than depicted in the two-dimensional figure. MRPP analysis of these seasonal groups confirmed their separation (overall *A* statistic = 0.0689, *p* = 0.0002; wet *vs.* early dry *A* = 0.0525, *p* = 0.0173; wet *vs.* late dry *A* = 0.0348, *p* = 0.0105; early *vs.* late dry *A* = 0.0726, *p* = 0.0007).

Figure 3. NMDS analysis of invertebrate data for October 1981–June 1984, showing significant seasonal groupings, indicated by MRPP analysis (see text). Proportion (%) of variance explained by each axis is shown. Stress = 0.088.
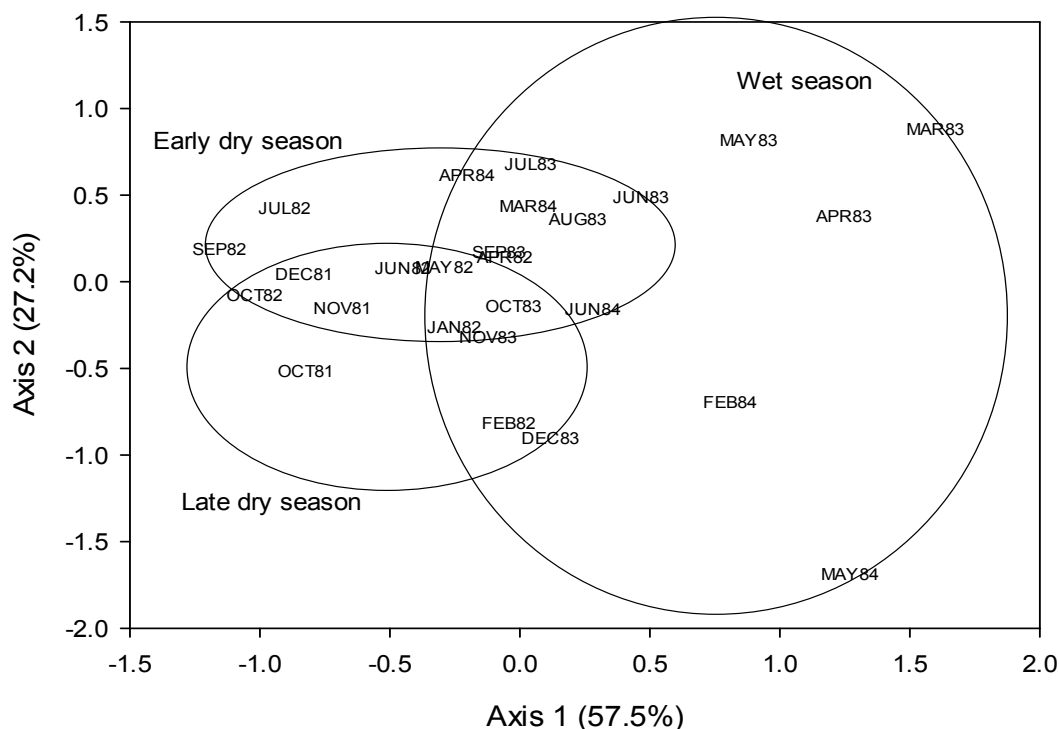
The NMDS analysis of family data for 1981 to 1995 indicated outliers on axis 1 from May 1984 and the three 1993–1995 samples (Figure 4a); MRPP analysis confirmed the separation of the decades (*A* = 0.1012, *p* < 0.0001). Axis 2 scores (Figure 4b) reflected antecedent rainfall, and therefore flows (Figure 4c), with correlations between scores and rainfall from the previous one month, three months and five months being, respectively: *r* = 0.578, *p* = 0.0010; *r* = 0.558, *p* = 0.0017; and *r* = 0.641, *p* = 0.0002. The outliers on axis 1 were placed unremarkably on axis 2.

The NMDS analysis of the first year's data showed that current velocity was the main correlate (d.f. = 182, *r* = 0.595, *p* < 0.0001), with CPOM (*r* = 0.251, *p* = 0.0006) and substratum particle size (*r* = 0.288, *p* <0.0001) also being significant, although *r²* values were low for the latter variables. Multiple regression analyses between counts of abundant species and major environmental variables showed little improvement over simple regressions with individual variables, so only the latter are reported here. From 183 samples and 60 common species, there were significant relationships (*p* < 0.05, albeit with modest *r²* values) with current velocity (25 positive, 11 negative), substratum particle size (7 positive, 9 negative) and litter (14 positive); 16 taxa showed no relationship with these variables (Table A2). Relationships typically aligned with known traits and habits. For example, taxa preferring high velocities included filterers (e.g., *Cheumatopsyche* and *Chimarra* species); and those avoiding high velocities included the shredders *Anisocentropus*, *Triplectides* and *Atalophlebia*, which also showed strong associations with CPOM *cf.* [6].

Figure 4. (**a**) Monthly NMDS axis 1 scores and (**b**) monthly NMDS axis 2 scores, over two decades; (**c**) one-month, three-month and five-month antecedent rainfall for each month.
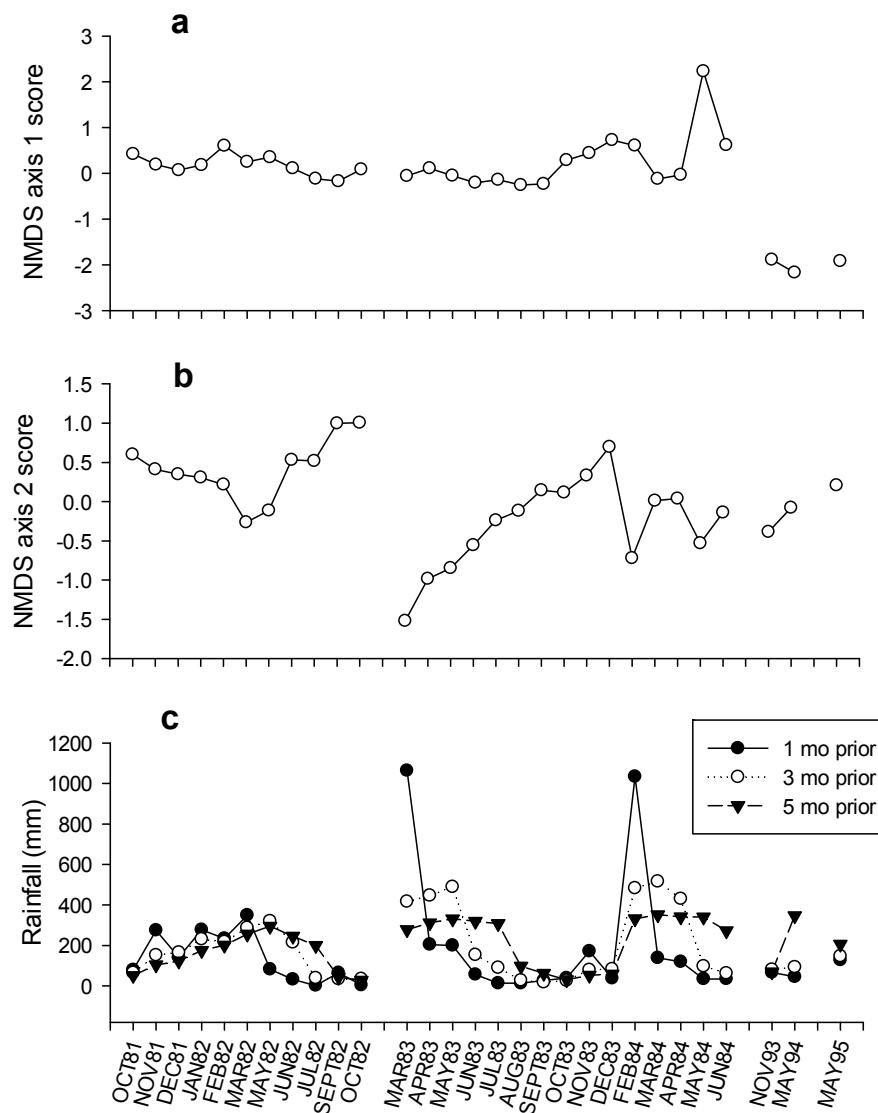
Indicator species analysis of the 1981–1982 seasonal groups showed that the early dry and late dry seasons were each characterised by several taxa, including three chironomids (not identified to species beyond this year) (Table 3). Similar analysis of the 1981–1984 seasonal groups showed distinctions between the late dry and wet seasons. The indicator species represented different trophic groups [6] and reflected seasonal change shown by the entire assemblage (Figures 3 and 4). Analysis of the 1981–1995 data, with "decade" (1980s *vs.* 1990s) as the grouping variable showed that significant indicator taxa for the 1980s were replaced by a few significant indicator taxa in the 90's, notably including three grazing taxa.

Trophic composition of the fauna from 1981–1984 showed cyclical changes with season, particularly driven by abundance of predators and detritivores (Figure 5). Ordination indicated that samples from the first two periods of the year largely separated from those of the last two periods (Figure 6). This was confirmed by MRPP analysis, with strong contrast among the four periods, especially between the first and second half of the year (for periods 1 + 2 *vs.* 3 + 4, $A = 0.1606$, $p = 0.0005$), largely driven by contrasts between periods 2 (late wet/early dry season) and 4 (late dry/early wet season) ($A = 0.2600$,

$p = 0.0003$). Regression analysis indicated associations between axis 1 and mean monthly temperature ($t_{28} = 2.35$, $p = 0.0269$) and rainfall ($t_{28} = -2.18$, $p = 0.0382$).

Table 3. Indicator values (IV) from indicator species analyses of groups of samples (**a**) from different seasons in 1981–1982; (**b**) from different seasons in 1981–1984; and (**c**) from the two decades. Only taxa for which $p < 0.05$ are shown. Abbreviations: "lv." = larvae; "ad." = adults.

	Time	Observed IV	Randomised IV	S.D.	*p*
(a) Seasons 81–82					
Helminthidae lv. sp. 7	Early dry	100	35.5	16.41	0.0076
Kiefferula sp. 1	Early dry	100	35.3	16.21	0.0076
Atalomicria	Early dry	40.4	36.8	1.84	0.0340
Philopotamidae	Early dry	41.7	37.5	2.19	0.0448
Helminthidae ad. sp. 5	Late dry	75	56.6	11.55	0.0204
Xenochironomus sp. 8	Late dry	81.3	37.8	15.4	0.0290
(b) Seasons 81–84					
Anura	Late dry	55.5	38.3	5.02	0.0016
Synlestidae	Late dry	63.7	32.2	8.33	0.0030
Leptophlebia sp.	Late dry	37	34.7	0.87	0.0034
Polycentropodidae	Late dry	48.7	40	3.65	0.0204
Chaoboridae	Late dry	47.7	24.5	8.98	0.0244
Muscidae	Late dry	40.5	19.9	8.67	0.0284
Ceratopogonidae	Late dry	52.9	40.5	5.57	0.0288
Glossosomatidae	Wet	55.5	33.3	10.52	0.0310
Simuliidae	Wet	53.4	42	5.6	0.0408
(c) Decades					
Eustheniidae	80's	100	55.1	6.8	0.0006
Leptophlebiidae	80's	65.5	52.6	2.1	0.0006
Odontoceridae	80's	100	54.6	6.13	0.0006
Ptilodactilidae	80's	100	58.3	9.02	0.0006
Caenidae	80's	96.2	55.9	9.64	0.0012
Helicopsychidae	80's	76.2	54.8	4	0.0016
Hydrochidae	80's	96.2	54.7	8.37	0.0018
Philorheithridae	80's	92.3	53.4	8.41	0.0028
Anura	80's	88.5	52.8	9.64	0.0052
Synthemidae	80's	88.5	52.6	9.71	0.0060
Decapoda	80's	80.8	50.5	11.46	0.0146
Ecnomidae	80's	81.3	55.8	9.31	0.0154
Aeschnidae	80's	70.7	56.7	5.34	0.0224
Philopotamidae	80's	73.8	58	6.25	0.0260
Cordulidae	90's	82.3	42.3	13.18	0.0006
Hydracarina	90's	97.7	34.7	11.84	0.0006
Libellulidae	90's	99.2	21.4	10.08	0.0006
Psephenidae	90's	91.7	56.9	11.97	0.0006
Pyralidae	90's	60.1	22.9	9.46	0.0082
Empididae	90's	63.7	24.3	11.38	0.0126
Hydroptilidae	90's	84.6	49.5	12.57	0.0162

Figure 5. Proportional trophic composition of monthly samples. "Grazers" include scrapers and grazers; "detritivores" are fine-particle collectors, gatherers and filterers; "shredders" are coarse-particle consumers; "predators" include predaceous filterers.
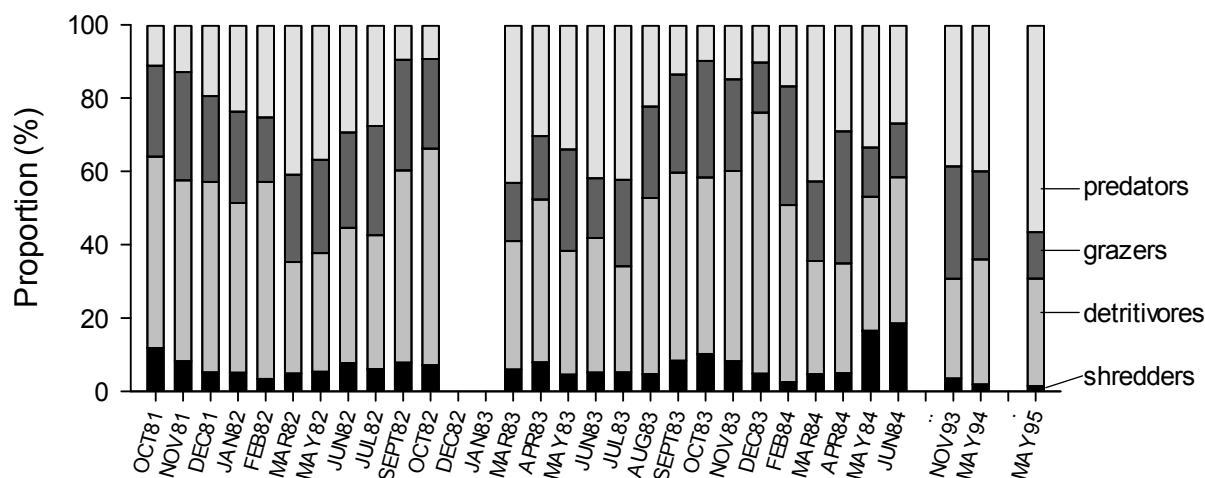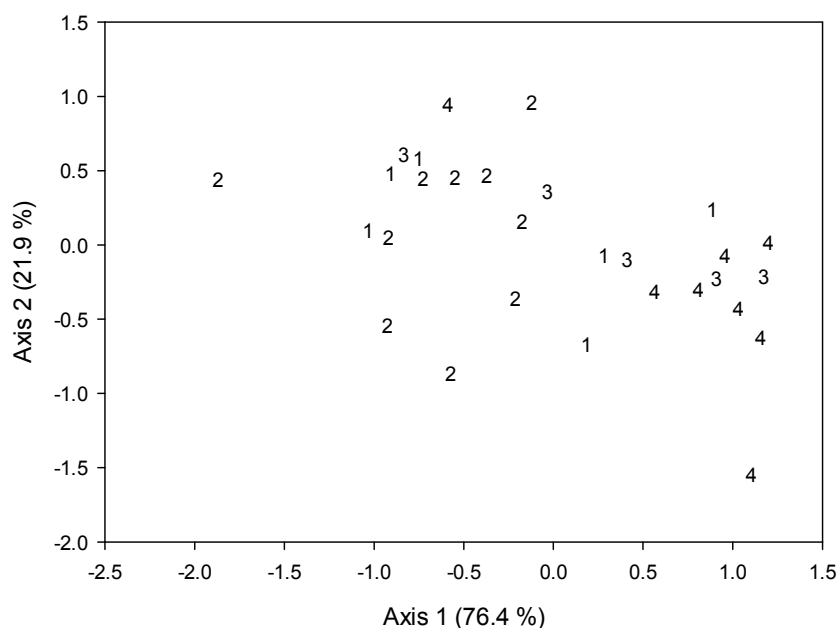

Figure 6. NMDS analysis of monthly trophic composition, with overlay (1–4) representing the four quarters of each year. Proportion (%) of variance explained by each axis is shown. Stress = 0.086.

4. Discussion

This study demonstrated strong seasonality in Yuccabine Creek, mainly relating to the flow regime and secondarily to temperature. Faunal attributes (population sizes, species richness, relative abundance of trophic groups, *etc.*) cycled seasonally, with variable disruption to assemblages during the wet season and, especially, as a result of an unexpected dry-season drought. Following disturbances, the fauna showed rapid recovery, although greater patchiness of some species persisted following the drought. There was a substantial shift in community composition (relative importance of species rather than gains or losses) between two decades, apparently due to opening of the riparian canopy by a cyclone.

The seasonality of flow was as expected for the Queensland Wet Tropics [17], although the partial drying of the stream was not. Most streams in the central Wet Tropics are perennial, and even streams only a few kilometres east of Yuccabine Ck., closer to the edge of the escarpment, appear to be perennial as they did not dry during this study and as they support obligate lotic taxa not present in Yuccabine Ck. (e.g., *Kirrara* nymphs, Ephemeroptera; unpublished data). Flow generally reflected the rainfall at Cardwell, but not always, given that the drought did not reflect antecedent Cardwell rainfall. Thus local variability in weather events can play a critical role in stream flow, particularly in small headwater streams [24].

Droughts and floods are the major forms of natural disturbance in flowing waters, often with one following the other—a "ramp disturbance" followed by a "pulse disturbance" [25]. The flow regime was clearly the dominant influence on the invertebrate fauna in Yuccabine Ck., as elsewhere in the seasonal [26–28] and aseasonal [29] tropics, and the seasonal responses of the fauna were strong. In the drying stream, overall density of the fauna increased as habitat area declined. Rapid recovery from disturbances indicated selected resistance/resilience traits [30–32] and drought refugia [4] that might include pools, sub-surface water, aerial adults or resistant eggs [13,33,34]. Unlike in other seasonal tropical streams [27,28] the three wet seasons sampled differed in abundance patterns—firstly, stable; secondly, rapid recovery from drought; and thirdly, variable in response to strong flows, with mean abundance similar to or less than the post-drought samples. The Wet Tropics stream fauna has been demonstrated experimentally to have high capacity to recolonise denuded substrata, particularly by drifting but also by means of upstream movements [5,35–37], from refugia, such as pools and mosses [38].

Patchiness following the drought reflects a common pattern in recovering streams [39]. However, total abundance masks individual species' patterns, which differed substantially in Yuccabine Ck. For example, different species of Chironomidae responded differently to seasonal change. Such differences reflect not only changing habitat conditions, but also differences in species' life histories and other traits [32]. Thus, many Wet Tropics species are continual breeders, but their rate of breeding is temperature-dependent, while other species are annual breeders [21,40], with mixed influence on the community. Continual breeders have most size classes present at any one time, whereas size-class distributions are skewed for annual breeders. Simple abundances cannot, therefore, completely reflect the make-up of the community at any one time as animals of different sizes will have different effects, both quantitative and qualitative, if their functional roles change with ontogeny. In this situation, functional diversity would be higher than a simple species count.

Species richness and evenness were stable except in response to drying and wet-season conditions. Several species of Chironomidae appeared and benefited from drying conditions, and increasing relative abundance of a few species led to decline in evenness. Drying also caused stream contraction and increased densities, which increased the chance of recording rarer species and, therefore, the species count, and the enhanced likelihood of inter- and intra-specific interactions [37]. In the wet season, fluctuations reflected high flows, which could tumble the substratum and remove litter packs [5,41]. Apparent loss of some species might also be due to emergence of annual breeders. Similarity between replicate sample units was marginally lower after the drought, indicating greater turnover or patchiness, but generally suggesting substantial stability in composition through the three years. Similarity between years was consistent and high [42]. Nevertheless, ordination of three years' samples clearly represented seasonal change, as would be expected from a seasonal site, and contrasting with the situation in aseasonal equatorial streams [15,16].

Individual species' occurrences were partly driven by habitat variables (current velocity, substratum, litter), as shown for mayflies in Yuccabine Ck. [43], and as reported elsewhere [44–48], though not universally [49]. Therefore, both spatial and temporal variables were predictors of the community structure [50,51]. Significant indicator-species scores highlighted changes mainly in relative abundance, not loss or gain of species. In 1981–1982, the main contrasting seasons were the early and late dry seasons, with switching of indicators as the extreme dry season progressed, culminating in drought. Seasonal switching was evident for 1981–1984, but separated late-dry and wet seasons, with low-flow specialists such as anurans and various Diptera contrasting with the high-flow specialist Simuliidae in the wet season. Between-decade contrast involved many taxa; notably, more grazers appeared in the 90's, apart from the Anura, which suffered serious declines in late 80's–early 90's as a result of the fungal disease chytridiomycosis [52,53]. The longer-term changes in the communities reflected, firstly, the greater openness of the canopy, with presumably greater primary production; and, secondly, samples taken following a poor wet season, indicating a need to take account of both current and antecedent conditions in interpreting sample results and to be aware of historical changes in the environment that can have continuing effects on the biota.

Stream food webs vary temporally and with habitat [6,9] and this was the case in Yuccabine Ck., as trophic characteristics of the community varied cyclically. Abundance data can mask the true trophic organisation of a community and biomass provides a better indication of functional relationships at any one time [6]. However, numerical abundance is useful in indicating change with time, as here. The abundance of predators has been noted previously for nearby streams [6] and is much greater than in some temperate streams [54], and attests to the high turnover of prey species, notably many of the smaller detrivorous and grazing insects [6]. Lower numbers of predators late in the year (the southern spring) may be due to high levels of emergence at this time of year [21]. Spates, causing widespread density-independent mortality, may reduce the importance of predation and competition as structuring forces in streams, at least in the wet season, although these factors may increase in importance as the dry season progresses, when habitats are reduced in extent and animal densities are higher [37,41,55].

5. Conclusions

Like temperate streams, there are various types of tropical stream, from aseasonal streams of uplands [56] and lowlands [15] to seasonal streams, also in uplands [6] and lowlands [55], and intermittent streams [13], with associated contrasts in their communities [16]. Yuccabine Ck. represents what is probably a common type of stream—seasonal upland—in much of the tropics [19]. Differences between this stream and temperate streams relate mainly to the higher temperatures of the tropics, allowing for continual breeding of many species [11,12], the generally higher diversity of invertebrates [19,57,58], and different patterns of leaf fall [59]. Otherwise, response to major drivers (flow, current velocity, substratum and litter accumulation) followed similar patterns to those typical of temperate streams [60].

Some metrics in Yuccabine Ck. indicated persistence and stability of the fauna, as reported elsewhere [7–9,54], even though some simple measures, such as richness, evenness and abundance, varied in space and time. However, this variation was predictable, with spatial patchiness and inter-sample variability greatest following high wet-season flows, and least in the dry season, even when approaching extreme drying. Not surprisingly, then, interpretation of invertebrate metrics in these streams needs to

account for seasonal change, especially antecedent flows, as would the sampling protocols for any monitoring program. Ecological studies need to take into account the significant variation in faunal densities that may occur over small spatial scales [2], and that individual riffles cannot readily "represent" stream sections or orders [3]. Multi-scale studies are required for better understanding of the spatial variation of macroinvertebrate communities and their relationship with the environment [1]. However, the data presented here suggest that, in the absence of human disturbance, biannual sampling—in the post-wet season/early dry season and mid-late dry season—would adequately characterise the fauna of the study site, which is similar to that of streams across the Wet Tropics [6]. Similar conclusions have been drawn for seasonal tropical streams elsewhere [27].

Acknowledgments

Appendix

Table A1. Rainfall at Cardwell, 1981–1995: total for each year and mean monthly totals for last few months of each year. Shaded cells are those where rainfall is below the 20th percentile. (Bureau of Meteorology data).

Year	Total Rain-Fall (mm)	Average Monthly Rainfall (mm)			
		August-December	September-December	October-December	November-December
1981	3615	122	149	165	208
1982	1750	49	52	48	70
1983	2012	58	69	83	105
1984	1987	39	48	64	83
1985	1448	76	94	122	119
1986	1378	68	77	88	118
1987	1593	81	95	110	154
1988	2051	201	244	320	473
1989	2333	126	149	197	237
1990	1940	34	42	51	74
1991	2725	24	28	38	55
1992	1801	128	156	165	237
1993	1434	82	91	95	95
1994	1998	33	39	46	46
1995	1354	71	66	85	79
Mean 1950–1996		85	99	122	153

Table A2. Correlations between abundances of invertebrate taxa and current velocity, maximum particle size of the substratum and CPOM cover of the substratum. Values of *r* given only where *p* < 0.05. Note that "significant" values range between equivalent r^2 values of only 0.023–0.336.

	Velocity	Particle	CPOM
Cheumatopsyche B	0.411	0.299	
Chimarra M	0.402	0.237	
Cheumatopsyche A	0.361		
Cosmioperla sp.	0.357		
Chimarra 7	0.348	0.161	
Illiesoperla sp.	0.317		
Austrolimnius lv 3	0.273		
Helicopsyche sp.	0.268		
Polycentropodidae 1	0.263		
Marilia sp.	0.250		
Cheumatopsyche C	0.243		
Asmicridea sp.	0.240		
Kingolus 4	0.234		
Helminthidae 2	0.224		
Nousia sp. 4	0.215		
Hydraenidae	0.212		
Ptilodactylidae	0.203	0.163	
Mecoptera	0.203	0.163	
Kingolus lv 2	0.182	0.187	
Kingolus lv 1	0.181		
Austrolimnius 6	0.178		
Austrolimnius 4	0.172	−0.163	
Austrolimnius 5	0.171	−0.280	
Simuliidae	0.161		
Dinotoperla sp.	0.157		
Austrolimnius ad 1	−0.152		
Ceratopogonidae	−0.192		0.164
Austrolimnius 1	−0.212	−0.183	0.304
Nousia 2	−0.213		0.475
Oecetis sp.	−0.262		0.465
Ulmerophlebia sp.	−0.268	−0.216	0.524
Anisocentropus sp.	−0.275		0.460
Nousia K	−0.287		0.187
Atalophebia sp.	−0.307	−0.296	0.580
Atalomicria sp.	−0.321		0.344
Triplectides sp.	−0.341		0.426
Polycentropodidae 7		0.171	0.187
Notalina sp.		−0.158	0.163
Rhagovelia sp.		−0.170	
Tasmanocoenis sp.		−0.244	
Austrophlebioides sp.		−0.299	
Nousia 1			0.331
Anura			0.187

Conflicts of Interest

The author declares no conflict of interest.

References

1. Boyero, L. Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecol. Res.* **2003**, *18*, 365–379.
2. Downes, B.J.; Lake, P.S.; Schreiber, E.S.G. Spatial variation in the distribution of stream invertebrates: Implications of patchiness for models of community organization. *Freshw. Biol.* **1993**, *30*, 119–132.
3. Downes, B.J.; Lake, P.S.; Schreiber, E.S.G. Habitat structure and invertebrate assemblages on stream stones: A multivariate view from the riffle. *Aust. J. Ecol.* **1995**, *20*, 502–514.
4. Lake, P.S. Ecological effects of perturbation by drought in flowing waters. *Freshw. Biol.* **2003**, *48*, 1161–1172.
5. Rosser, Z.; Pearson, R.G. Responses of rock fauna to physical disturbance in two Australian tropical rainforest streams. *J. N. Am. Benthol. Soc.* **1995**, *14*, 183–196.
6. Cheshire, K.; Boyero, L.; Pearson, R.G. Food webs in tropical Australian streams: Shredders are not scarce. *Freshw. Biol.* **2005**, *50*, 748–769.
7. Townsend, C.R.; Hildrew, A.G.; Schofield, K. Persistence of stream invertebrate communities in relation to environmental variability. *J. Anim. Ecol.* **1987**, *56*, 597–613.
8. Hildrew, A.G.; Giller, P.S. Patchiness, species interactions and disturbance in the stream benthos. In *Aquatic Ecology: Scale, Pattern and Process*; Giller, P.S., Hildrew, A.G., Raffaelli, D.G., Eds.; Symposium of the British Ecological Society, Blackwell: Oxford, UK, 1994; pp. 21–62.
9. Woodward, G.; Jones, J.I.; Hildrew, A.G. Community persistence in Broadstone Stream (UK) over three decades. *Freshw. Biol.* **2002**, *47*, 1419–1435.
10. Dudgeon, D. (Ed.) *Tropical Stream Ecology*; Academic Press: London, UK, 2008.
11. Boulton, A.J.; Boyero, L.; Covich, A.P.; Dobson, M.K.; Lake, P.S.; Pearson, R.G. Are tropical streams ecologically different from temperate streams? In *Tropical Stream Ecology*; Dudgeon, D., Ed.; Academic Press: San Diego, CA, USA, 2008; pp. 257–284.
12. Boyero, L.; Ramírez, A.; Dudgeon D.; Pearson, R.G. Are tropical streams ecologically different? *J. N. Am. Benthol. Soc.* **2009**, *28*, 397–403.
13. Smith, R.E.W.; Pearson, R.G. The macro-invertebrate communities of temporary pools in an intermittent stream in tropical Queensland. *Hydrobiologia* **1987**, *150*, 45–61.
14. Townsend, S.A.; Douglas, M.M. The effect of three fire regimes on stream water quality, water yield and export coefficients in a tropical savanna (northern Australia). *J. Hydrol.* **2000**, *229*, 118–137.
15. Yule, C.M. Benthic invertebrate fauna of an aseasonal tropical mountain stream on Bougainville Island, Papua New Guinea. *Mar. Freshw. Res.* **1995**, *46*, 507–518.
16. Yule, C.M.; Pearson, R.G. Aseasonality of benthic invertebrates in a tropical stream on Bougainville Island, Papua New Guinea. *Arch. Hydrobiol.* **1996**, *137*, 95–117.

17. Kennard, M.J.; Pusey, B.J.; Olden, J.D.; Mackay, S.J.; Stein, J.L.; Marsh, N. Classification of natural flow regimes in Australia to support environmental flow management. *Freshw. Biol.* **2010**, *55*, 171–193.

18. Petherham, C.; McMahon, T.A.; Peel, M.C. Flow characteristics of rivers in northern Australia: Implications for development. *J. Hydrol.* **2008**, *357*, 93–111.

19. Pearson, R.G.; Benson, L.J.; Smith, R.E.W. Diversity and abundance of the fauna in Yuccabine Creek, a tropical rainforest stream. In *Limnology in Australia*; De Deckker, P., Williams, W.D., Eds.; CSIRO: Melbourne, Australia, 1986; pp. 329–342.

20. McNeil, V.H.; Cox, M.E.; Preda, M. Assessment of chemical water types and their spatial variation using multi-stage cluster analysis, Queensland, Australia. *J. Hydrol.* **2005**, *310*, 181–200.

21. Benson, L.J.; Pearson, R.G. Diversity and seasonality of adult Trichoptera captured in a light-trap at Yuccabine Creek, a tropical Australian rainforest stream. *Aust. J. Ecol.* **1988**, *13*, 337–344.

22. Foggo A.; Rundle S.D.; Bilton D.T. The net result: Evaluating species richness extrapolation techniques for littoral pond invertebrates. *Freshw. Biol.* **2003**, *48*, 1756–1764.

23. McCune, B.; Mefford, M.J. *PC-ORD Multivariate Analysis of Ecological Data. Version 6.06*; MjM Software: Gleneden Beach, OR, USA, 2011.

24. Soulsby, C.; Pomeroy, A.; Gibbins, C. Hydrology and hydrochemistry of a montane rainforest catchment in Queensland, Australia. In *Hydrochemistry: Proceedings of the Rabat Symposium April 1997*; Internat. Assoc. Hydrol. Sci. Publication: 1997; Volume 244, pp. 297–307.

25. Lake, P.S. Disturbance, patchiness, and diversity in streams. *J. N. Am. Benthol. Soc.* **2000**, *19*, 573–592.

26. Dudgeon, D. Longitudinal and temporal changes in functional organization of macroinvertebrate communities in the Lam Tsuen River, Hong Kong. *Hydrobiologia* **1984**, *111*, 207–217.

27. Leung, A.S.L.; Dudgeon, D. Scales of spatiotemporal variability in macroinvertebrate abundance and diversity in monsoonal streams: Detecting environmental change. *Freshw. Biol.* **2011**, *56*, 1193–1208.

28. Leung, A.S.L.; Li, A.O.Y.; Dudgeon, D. Scales of spatiotemporal variation in macroinvertebrate assemblage structure in monsoonal streams: The importance of season. *Freshw. Biol.* **2012**, *57*, 218–231.

29. Rawi, C.S.M.; Al-Shami, S.A.; Madrus, M.R.; Ahmad A.H. Biological and ecological diversity of aquatic macroinvertebrates in response to hydrological and physicochemical parameters in tropical forest streams of Gunung Tebu, Malaysia: Implications for ecohydrological assessment. *Ecohydrology* **2014**, *7*, 496–507.

30. Poff, N.L. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* **1997**, *16*, 391–409.

31. Griswold, M.W.; Berzinis, E.W.; Crisman, T.L.; Golladay, S.W. Impacts of climatic stability on the structural and functional aspects of macroinvertebrate communities after severe drought. *Freshw. Biol.* **2008**, *53*, 2465–2483.

32. Chessman, B.C. Relationships between lotic macroinvertebrate traits and responses to extreme drought. *Freshw. Biol.* **2014**, doi:10.1111/fwb.12466.

33. Hynes, H.B.N. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.* **1961**, *57*, 344–388.

34. Morrison, B.R.S. Recolonisation of four small streams in central Scotland following drought conditions in 1984. *Hydrobiologia* **1990**, *208*, 261–267.

35. Wulf, P.L. Bryophytes in streams: Habitat refuge for aquatic invertebrates. Honours Thesis, James Cook University, Townsville, Australia, 1999.

36. Benson, L.J.; Pearson, R.G. Drift and upstream movements of macro-invertebrates in a tropical Australian stream. *Hydrobiologia* **1987**, *153*, 225–239.

37. Benson, L.J.; Pearson, R.G. The role of drift and effect of season in colonization of implanted substrata in a tropical Australian stream. *Freshw. Biol.* **1987**, *18*, 109–116.

38. Connolly, N.M.; Christidis, F.; McKie, B.; Boyero, L.; Pearson, R.G. Diversity of invertebrates in Wet Tropics streams: Patterns and processes. In *Living in a Dynamic Tropical Forest Landscape*; Stork, N.E., Turton, S., Eds.; Blackwells Publishing: Oxford, UK, 2008; pp. 161–177.

39. Olsen, D.A.; Matthaei, C.D.; Townsend, C.R. Patch history, invertebrate patch dynamics and heterogeneous community composition: Perspectives from a manipulative stream experiment. *Mar. Freshw. Res.* **2007**, *58*, 307–314.

40. Sheldon, A.L.; Theischinger, G. Stoneflies (Plecoptera) in a tropical Australian stream: Diversity, distribution and seasonality. *Illiesia* **2009**, *5*, 40–50.

41. Pearson, R.G. Biodiversity of the freshwater fauna of the Wet Tropics region of north-eastern Australia: Patterns and possible determinants. In *Tropical Rain Forests: Past, Present and Future*; Bermingham, E., Dick, C.W., Moritz, C., Eds.; University of Chicago Press: Chicago, IL, USA, 2005; pp. 470–485.

42. Mykra, H.; Heino, J.; Oksanen, J.; Muotka, T. The stability-diversity relationship in stream macroinvertebrates: Influences of sampling effects and habitat complexity. *Freshw. Biol.* **2011**, *56*, 1122–1132.

43. Hearnden, M.R.; Pearson, R.G. Habitat partitioning among mayflies (Insecta: Ephemeroptera) in an Australian tropical stream. *Oecologia* **1991**, *87*, 91–101.

44. Erman, D.C.; Erman, N.A. The response of stream macroinvertebrates to substrate size and heterogeneity. *Hydrobiologia* **1984**, *108*, 75–82.

45. Cummins, K.W.; Lauff, G.F. The influence of substratum particle size on the distribution of stream benthos. *Hydrobiologia* **1969**, *34*, 145–181.

46. Rabeni, C.F.; Minshall, G.W. Factors affecting the microdistribution of stream benthic insects. *Oikos* **1977**, *29*, 33–43.

47. Minshall, G.W. Aquatic insect-substratum relationships. In *The Ecology of Aquatic Insects*; Resh, V.H., Rosenberg, D.M., Eds.; Praeger: New York, NY, USA, 1984; pp. 358–400.

48. Doisy, K.E.; Rabeni, C.F. Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *J. N. Am. BenthOL. Soc.* **2001**, *20*, 17–32.

49. Lancaster, J.; Downes, B.J.; Glaister, A. Interacting environmental gradients, trade-offs and reversals in the abundance-environment relationships of stream insects: When flow is unimportant. *Mar. Freshw. Res.* **2009**, *60*, 259–270.

50. Göthe, E.; Angeler, D.G.; Sandin, L. Metacommunity structure in a small boreal stream network. *J. Anim. Ecol.* **2013**, *82*, 449–458.

51. Heino, J.; Grönroos, M. Untangling the relationships among regional occupancy, species traits, and niche characteristics in stream invertebrates. *Ecol. Evol.* **2014**, *4*, 1931–1942.

52. McDonald, K.; Alford, R.A. A review of declining frogs in northern Queensland. In *Declines and Disappearances of Australian Frogs*; Cambell, A., Ed.; Commmonwealth of Australai: Canberra, Australia, 1999; pp. 14–22.

53. Skerratt, L.F.; Berger, L.; Speare, R.; Cashins, S.; McDonald, K.R.; Phillott, A.D.; Hines, H.D.; Kenyon, N. Spread of Chytridiomycosis has caused the rapid globalm decline and extinction of frogs. *EcoHealth* **2007**, *4*, 125–134.

54. Lake, P.S. The macroinvertebrate community of stones in an Australian upland stream. *Verh. Int. Ver. Limnol.* **1985**, *22*, 2141–2147.

55. Dudgeon, D. The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. *Freshw. Biol.* **1993**, *30*, 189–97.

56. Turcotte, P.; Harper, P.P. The macro-invertebrate fauna of a small Andean stream. *Freshw. Biol.* **1982**, *12*, 411–419.

57. Lake, P.S.; Schreiber, E.S.G.; Milne, B.J.; Pearson, R.G. Species richness in streams: Patterns over time, with stream size and with latitude. *Verh. Int. Ver. Limnol.* **1994**, *25*, 1822–1826.

58. Pearson, R.G.; Boyero, L. Gradients in regional diversity of freshwater taxa. *J. N. Am. Benthol. Soc.* **2009**, *28*, 504–514.

59. Benson, L.J.; Pearson, R.G. Litter inputs to a tropical Australian upland rainforest stream. *Aust. J. Ecol.* **1993**, *18*, 377–383.

60. Cobb, D.G.; Galloway, T.D.; Flannagan, J.F. Effects of discharge and substrate stability on density and species composition of stream insects. *Can. J. Fish Aquat. Sci.* **1992**, *49*, 1788–1795.