Hydrobiologia (2010) 641:85–95
DOI 10.1007/s10750-009-0059-4

PRIMARY RESEARCH PAPER

Effect of spates and land use on macroinvertebrate community in Neotropical Andean streams

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Received: 27 April 2009 / Revised: 7 December 2009 / Accepted: 14 December 2009 / Published online: 11 January 2010

Abstract The aim of this study was to determine the effect of monsoonal spates and land uses on abundance, richness, diversity, and evenness of benthic macroinvertebrates in streams, and whether these factors interacted with each other to influence community structure. Two groups of streams with different underlying disturbance profiles were studied. One group was in a native forest (non-degraded area) and experienced only spate, and the other group drained an area degraded by agriculture and cattle grazing, and so was subject to two types of disturbances. Spates produced a strong decline in invertebrate abundance and an increase in evenness, whereas changes in land uses caused an increase in abundance of tolerant taxa and a significant decline in richness, diversity, and evenness. Differences in richness and Oligochaeta abundance between land uses were mostly evident in the pre-spate period due to low water levels magnifying some physicochemical changes caused by ecosystem degradation. Canonical correspondence analysis indicated that degraded sites had the highest conductivity, nitrate, pH, and water temperature. Upstream non-degraded streams generally exhibited higher dissolved oxygen values. Taxa such as Psychodidae and Tipulidae, *Camelobaetidius penai*, *Austrelmis* spp. (adult), *Macrelmis* spp. (adult), and *Marilia* spp. dominated in non-degraded sites, while *Tricorythodes popayanicus*, *Caenis ludicra*, *Dodecabates dodecaporus*, *Atractides* sp., and *Torrenticola columbiana* were abundant in downstream degraded streams. These two groups of taxa may be useful biological indicators of water quality in streams of northwestern Argentina.

Keywords Anthropogenic impacts · Disturbance · Floods · Land use · Northwestern Argentina · Subtropical climate

Electronic supplementary material The online version of this article (doi:10.1007/s10750-009-0059-4) contains supplementary material, which is available to authorized users.

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Introduction

Disturbance is one of the dominant forces affecting community structure in many ecological systems (Wootton, 1998; Lake, 2000). In aquatic systems, included in the primary potential agents of disturbance are spates. Resh et al. (1988) are quite insistent that spates impact structural and functional components of stream biotas, which may play a role in the evolution of these organisms. Sub-tropical areas with monsoonal climates experience some of the largest floods on earth (Gupta, 1987). Floods and spates in such areas are qualified as disturbances due to their large magnitude and geomorphological effect, but they are highly predictable (Resh et al., 1988). During high flow events, high shear forces suspend sediments, move bottom materials, and kill or displace stream biota (Lake, 2000). Furthermore, various aspects of diversity (i.e., abundance and species richness) may respond differently to this disturbance (Death & Winterbourn, 1995; Death, 1996). Most authors have found significant decreases in the mean abundance of benthic organisms after spates (e.g., Bond & Downes, 2003; Melo et al., 2003). However, species richness can decrease (Death & Winterbourn, 1995; Death, 1996, 2002; Effenberger et al., 2008) or remain constant (Reice, 1985; Rempel et al., 1999) following floods. Proposed mechanisms by which populations persist in hydrologically disturbed environments include morphological, behavioral, and physiological traits (Wallace & Anderson, 1996; Lytle & Poff, 2004), and the use of flow refugia (Matthaei et al., 2000; Negishi & Richardson, 2006).

In the northwestern region of Argentina, the combination of a monsoonal climate with steep slopes results in large and seasonally predictable spates (Fernández, 2003). Superimposed upon this regime are the impacts of agriculture and cattle grazing, which strongly influence rates and trajectories of postdisturbance community recovery. Increased extension of agricultural and cattle lands have affected the water quality, physical habitat, and biota of many streams of northwestern Argentina (Fernández & Molineri, 2006; Von Ellenrieder, 2007; Fernández et al., 2009; Sirombra & Mesa, 2009). Grazing and trampling are the most extensive degradation factors in this region (Grau & Brown, 2000). Heavily shaded native forested streams have been converted into open waterways that are often grazed until to the channel edge by goats and cattle resulting in bank erosion and higher temperatures and nutrient inputs (Fernández et al., 2009). These land-use changes constitute another type of disturbance and can continue to affect stream community structure and function over the long term (Lake, 2000).

Owing to the increasing anthropogenic impacts that affect the streams of this subtropical region of Argentina, any assessments of change in community structure in conjunction with the monsoon would thus ideally involve comparison between catchments under different land uses. In this sense, in order to analyze the individual and interactive effect of monsoonal spates and land-use change on macroinvertebrate communities, I examined two groups of streams with different underlying disturbance profiles. One group was in a native forest and so experienced only one type of disturbance, and the other group drained an area degraded by agriculture and cattle grazing and so was subject to two types of disturbances. I hypothesized that (1) land-use change would affect environmental characteristics of streams (physical and chemical variables); (2) these abiotic changes would influence community structure and composition (reduce abundance, richness, diversity, and evenness, and change in community composition from one dominated by sensitive species to one composed by tolerant ones); (3) monsoonal spates would reduce abundance, richness, diversity, and evenness; and (4) the effects of spates on these community metrics would be greater than the effect of land use. The last hypothesis was related with the tested catastrophic effect of the peak of discharge on arthropod assemblages of Lules river basin (Mesa et al., 2009).

Methods

Study area

This study was conducted in Lules river basin, a seventh-order catchment located in Tucumán province in the northwestern of Argentina (Fig. 1). This region is characterized by the monsoon, a rainy season that lasts from November to April, during which 80–90% of annual rainfall occurs (Fig. 2). The maximum average precipitation and discharge are in January, with values of 226 mm and 20 m^3/s, respectively (Fig. 2). The dry period extends from April to October (autumn/winter season), with minimum average values of rainfall (11.8 mm) and discharge (4.64 m^3/s) in August (data recorded by Obispo Colombres, meteorological station of Tucumán province, period 1961–1990). Five non-degraded sites were located in the upper part of the basin (925–1,360 m.a.s.l) (sites 1–5, Fig. 1). Here, riparian vegetation was composed by native species belonging to the Yungas phytogeographical province. A mixture of native shrubs (e.g., *Verbesina suncho, Eupatorium lasiophtalmun*, *Pisoniella arborescens*) and native trees (e.g., *Acacia praecox, Celtis iguanaea*, *Juglans australis*, *Myrsine laetevirens*, *Parapiptadenia excelsa*, *Cinnamomum*

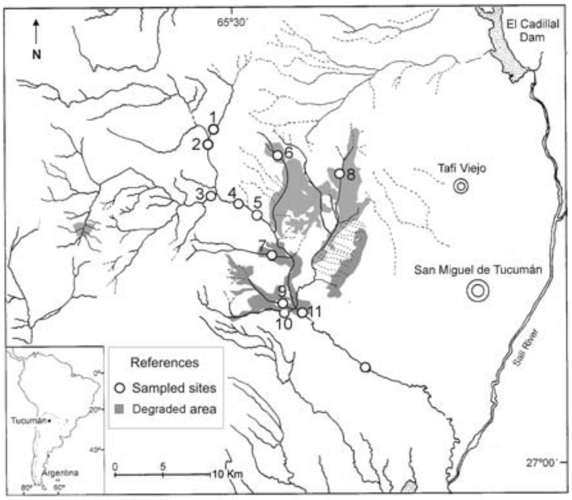

Fig. 1 Map of Lules river basin showing the sampled sites and the degraded area by agriculture and cattle grazing. Sites 1–5, non-degraded sites; 6–11, degraded sites

porphyrium, *Eugenia uniflora*, *Zanthoxilum fagara*) dominated these sites (Sirombra & Mesa, 2009). Other six streams (sites 6–11, Fig. 1) were situated in the lower part of the basin (650–1,080 m.a.s.l). The riparian area of these sites was greatly impacted by the over grazing of cattle and goats. Fragments of exotic vegetation interdispersed by pasture area occurred in this zone. The exotic vegetation included *Citrus aurantium*, *Ligustrum lucidum*, *Gleditsia triacanthos*, *Morus alba*, *Pinus taeda*, and *Pyracantha angustifolia* species (Sirombra & Mesa, 2009). The extension of agricultural and cattle lands comprised almost the 30% of the middle-lower area of the basin and four sub-basins (Mesa, 2006): Siambón (related with site 6), impacted area = 38%; Potrerillo (site 7) = 8.3%; San Javier (site 8) = 19%; and Tablas (site 9 and 10) = 9% (Fig. 1).

Benthic sampling

The 11 sites were sampled in pre-spate (September 2005, September 2006) and post-spate (March 2006, March 2007) periods. Three Surber samples (area 0.09 m^2, mesh size 300 μm) were taken from riffle habitats. Benthic sampling of sites 2, 4, and 5 in March 2006 and on site 3 in March 2007 could not be carried out because of high water levels. Samples were preserved in the field in 4% formalin, and sorted and identified in the laboratory. Identifications were made to the lowest taxonomic group possible.

Statistical analysis

For each sampled stream and each date, mean abundance, richness, exp Shannon index of species diversity, and Shannon index of evenness of invertebrates were calculated according to Magurran (1989) and Gray (2000). Species richness is strongly affected by the number of individuals in a sample

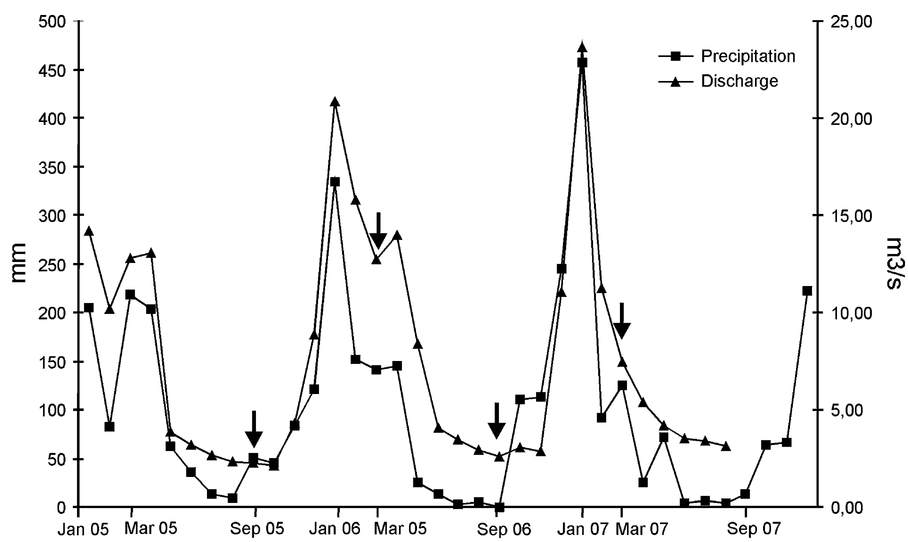

Fig. 2 Hydrograph of mean monthly discharge and precipitation during the period 2005–2007. *Arrows* indicate month when benthic sampling was carried out

(Gotelli & Colwell, 2001). Accordingly, patterns obtained using raw species richness may reflect high density in the patch and, thus, a sampling artifact (McCabe & Gotelli, 2000; Melo et al., 2003). In order to remove the effect of sample abundance on species richness, I carried out the analysis using rarefied species richness as the response. The number of taxa found in this study was calculated for a common abundance level (300 individuals) using the computer Biodiversity Professional, version 5.0 (Mc Aleece, 1997). Three-hundred individuals were chosen as a cut-level for inclusion in the taxon richness analysis, since this is a sufficiently large number of individuals for comparison of taxon richness in fixed count studies (Vinson & Hawkins, 1996).

In order to assess changes in mean abundance, richness, diversity, evenness, and mean abundance of abundant taxa (abundance >2%), one-way ANOVAs were conducted between seasons and land uses (degraded vs. non-degraded sites). Invertebrate abundance data were $\log_{10}(x + 1)$ transformed before this analysis to meet assumptions of homogeneity of variance and normality (Zar, 1996). Changes in community structure (random factors) were compared between land-uses and seasons (fixed factors) simultaneously using crossed ANOVAs, based on General Linear Model (GLM). This method allowed the significance of each factor to be assessed whilst holding constant the variation due to the other factors. The interaction between land use and season indicated whether seasonal patterns varied across land-use types.

The ordination technique of canonical correspondence analysis (CCA) (CANOCO 3.0; ter Braak & Smilauer, 1998) was used to examine the variation in macroinvertebrate community composition in relation to the measured environmental variables. In order to focus on land-use effects (absent of monsoonal spates), only pre-spate samples were included in the analysis. All the measured environmental variables (27) from each site were used initially. The number of environmental variables was then reduced eliminating those variables highly intercorrelated with others (inflation factor >20), leaving a total of eight variables. The variables selected were water temperature ($T°$), dissolved oxygen (DO), discharge (Q), nitrate (NO), percentage area of the sub-basin affected by agriculture, and cattle grazing (%A), pH, channel width (CW), and conductivity (Cond). Forward selection was carried out on its remaining variables to identify those that explained a significant ($P < 0.05$ using 999 Monte Carlo permutations) amount of variation in the community assemblages. All the environmental variables (except pH) were $\log_{10}(x + 1)$ transformed.

Results

Effect of monsoonal spates and land uses on community metrics

There were significant differences in the abundance of invertebrate assemblages between seasons (ANOVA, $F_{1,39} = 17.29$, $P < 0.001$) and land uses (ANOVA, $F_{1,39} = 5.73$, $P < 0.05$) but not in the land use/season interaction (ANOVA, $F_{1,39} = 0.5$, $P > 0.05$) (Table 1). Compared to the effect of land use, season had a stronger effect on invertebrate abundance: mean abundance was almost three times higher in the pre-spate period compared with post-spate, and about two times higher in degraded than non-degraded sites.

Mean richness differed strongly between land uses (ANOVA, $F_{1,39} = 13.25$, $P < 0.001$) being higher in non-degraded than degraded streams. No significant change was detected in this parameter between seasons (ANOVA, $F_{1,39} = 0.01$, $P > 0.05$). The interactive parameter land use/season was significant (ANOVA, $F_{1,39} = 5.3$, $P < 0.05$): a strong difference in invertebrate richness was detected in the pre-spate period between non-degraded and degraded streams (ANOVA, $F_{1,21} = 16.7$, $P < 0.001$, Table 2), whereas other combinations between these two factors were not significant (Table 2).

Exp Shannon diversity differed significantly between land uses (ANOVA, $F_{1,39} = 11.3$, $P < 0.01$), being higher in non-degraded than degraded sites. No significant change was detected between seasons (ANOVA, $F_{1,39} = 0.30$, $P > 0.05$) and in the land use/season interaction term (ANOVA, $F_{1,39} = 0.02$, $P > 0.05$) (Table 1).

Compared with the effect of season, land use had a stronger effect on invertebrate evenness. Evenness was significantly higher in non-degraded sites (ANOVA, $F_{1,39} = 13.4$, $P < 0.01$), and in the post-spate season (ANOVA, $F_{1,39} = 5.62$, $P < 0.05$) (Table 1).

Except *Baetodes huaico*, the spate produced a strong significant decline on all taxa: mean

Table 1 Mean macroinvertebrate abundance, mean taxa richness, exp Shannon index of diversity, and evenness between seasons and land uses ($n = 40$), and results of ANOVA (F) between seasons, land use, and the interaction between these two factors using crossed factorial GLM

	Pre-spate	Post-spate	Non-degraded	Degraded	Season	Land use	Season × land use
Abundance	6736 (6513)	2537 (1510)	2802 (1959)	6018 (6723)	17.29***	5.73*	0.5
Richness	24.7 (5.6)	24.6 (3.5)	27.6 (3.6)	22.8 (4.4)	0.01	13.25***	5.3*
Exp Shannon	7.35 (2.7)	7.86 (2.4)	9.3 (2.4)	6.2 (1.7)	0.30	11.03**	0.02
Evenness	0.25 (0.05)	0.27 (0.05)	0.28 (0.04)	0.24 (0.05)	5.62*	13.4**	0.18
Austrelmis spp. (larvae)	265 (387)	39 (48)	186 (220)	144 (339)	7.58**	2.55	0.00
Baetodes huaico	362 (549)	474 (498)	253 (243)	495 (604)	0.78	0.60	0.78
Orthocladiinae	1654 (1340)	309 (491)	611 (911)	1223 (1322)	27.07***	5.27*	0.25
Chironominae	617 (757)	415 (1339)	158 (181)	703 (1262)	17.67***	4.49*	0.15
Oligochaeta	2367 (3954)	41(74)	10 (13)	1898 (3621)	16.1***	28.06***	5.27*

Values of standard deviations are in parenthesis

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

abundance of *Austrelmis* spp. (larvae), Orthocladiinae, and Chironominae were among 2–7 times higher in the pre-spate than in the post-spate period, whereas the abundance of Oligochaeta was 57 times higher in the pre-spate compared with the post-spate season (Table 1). Mean abundance of Orthocladiinae and Chironominae differed significantly between land uses, being higher in degraded than non-degraded streams (ANOVA, $P < 0.05$, Table 1), and the effect of this factor was stronger with Oligochaeta, which had an abundance 18 times higher in degraded than non-degraded sites. The land use/season interaction term was also significant for this taxon: mean abundance of Oligochaeta differed significantly between degraded and non-degraded sites in both seasons, but in the pre-spate period, the effect of land use was stronger (ANOVA, $F_{1,18} = 27.78$, $P < 0.001$) than in the post-spate season (ANOVA, $F_{1,16} = 5.01$, $P < 0.05$) (Table 2). Mean abundance of this taxon differed significantly between seasons in degraded sites (ANOVA, $F_{1,23} = 25.06$, $P < 0.001$), being higher in the pre-spate period than in the post-spate period (Table 2).

Effects of land use on community composition

The first two CCA axes accounted for 41% of the total variance in the species data (Fig. 3A, B), whereas the accumulative variation explained by these axes of the taxa–environment relationship was 63%. Monte Carlo global permutation tests also demonstrated a significant macroinvertebrate environment relationship ($P < 0.01$) along the first axis (F ratio = 6.43, $P = 0.0001$) and subsequent canonical axes (F ratio = 3.41, P ratio = 0.0001). Intraset correlations of environmental variables with the first two axes of CCA and significance levels based on stepwise addition of the respective variables to the ordination (conditional effect) are shown in Table 3. Five variables were retained as significant in the CCA with forward selection of the eight environmental variables (Table 3). The three variables that explained more than 10% of the variation were conductivity (38%), channel width (15%), and water temperature (11%). Discharge (7.6%), percentage area affected by agricultural and cattle grazing (7.6%), nitrate (7.6%), dissolved oxygen (7.6%), and pH (3.8%) explained less than the 10% of the variation (Table 3). Increased conductivity, pH, nitrate, water temperature, and the greater area affected by agricultural and cattle grazing were positively associated with invertebrate taxa such as *Caenis ludicra*, *Tricorythodes popayanicus*, *Dodecabates dodecaporus*, *Atractides* sp., and *Torrenticola columbiana* (Fig. 3A, B). These characteristics correspond to degraded sites (right side of the biplot, Fig. 3A). The left side of the biplot corresponded to non-degraded sites. These sites were characterized by high dissolved oxygen levels and discharge (Fig. 3A). Sites in this category were dominated by individuals of the Psychodidae and Tipulidae dipteran families,

Table 2 Interaction between land use/season of mean taxa richness and mean abundance of Oligochaeta using crossed ANOVAs based on general linear model (GLM)

	Pre-spate			Post-spate			Non-degraded			Degraded		
	Non-degraded	Degraded	*F*	Non-degraded	Degraded	*F*	Pre-spate	Post-spate	*F*	Pre-spate	Post-spate	*F*
Richness	24.5 (5.8)	23.5 (3.6)	16.7***	25.6 (5.2)	25.5 (4.6)	0.67	24.5 (5.8)	25.6 (5.2)	3.49	23.5 (3.7)	25.5 (4.6)	2.52
Oligochaeta	12.9 (15.3)	3740 (4473)	27.78***	5.4 (8)	55.4 (84.6)	5.01*	12.9 (15)	5.4 (8)	2.06	3740 (4473)	55 (85)	25.06***

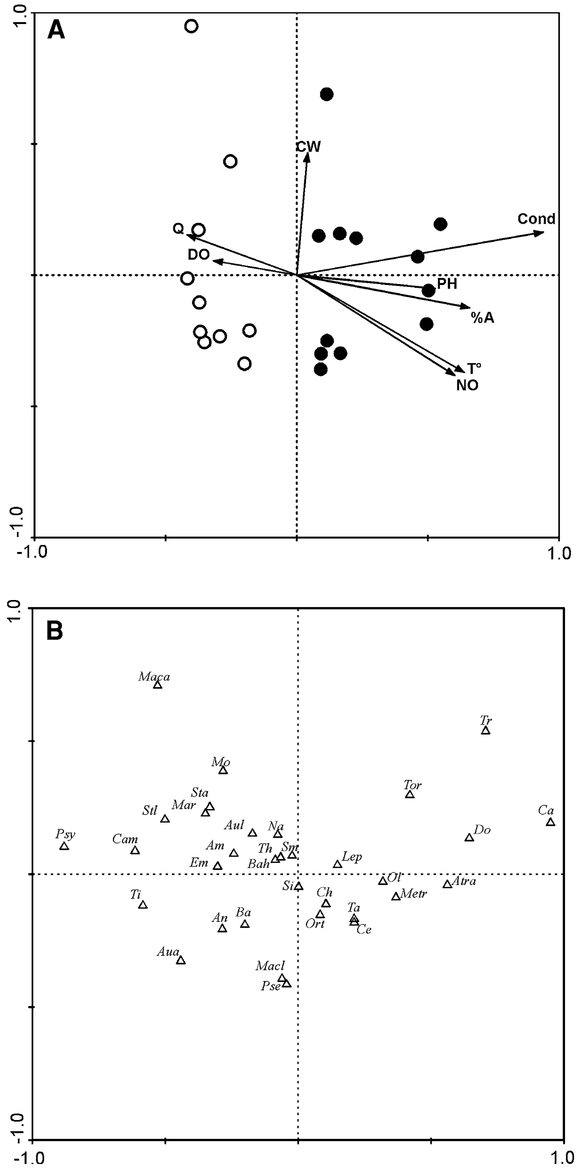

Fig. 3 **A** Ordination diagram (canonical correspondence analysis) of non-degraded ($n = 10$, *open circles*), degraded sites ($n = 12$, *closed circles*), and environmental variables (*arrows*). Variables references: *DO* dissolved oxygen, *T*° water temperature, *NO* nitrate, *%A* percentage of the sub-basin affected by land-use practices, *Cond* conductivity, *Q* discharge, and *CW* channel width. **B** Species ordination. Full names of taxa codes are given in Appendix 1—Supplementary Material

Camelobaetidius penai mayfly, coleopteran taxa such as Staphylinidae (larvae and adult), *Austrelmis* spp. (adult), *Macrelmis* spp. (adult), and *Marilia* sp. caddisfly (Fig. 3B).

Table 3 Mean values and standard deviation (in parenthesis) of environmental variables measured in non-degraded ($n = 16$) and degraded ($n = 24$) sites, and percentage of explained variation of species data by individual environmental variables using CCA in which one environmental variable constrained the ordination

Variables	Non-degraded	Degraded	%	*P*
Conductivity (μS/cm)	126 (27.9)	499 (282)	37.9	6.67***
Channel width (m)	7 (4.5)	6 (3.8)	15.2	1.82
Water temperature (°C)	17 (4.5)	19 (3.8)	11.4	6.38***
Discharge (m^3/s)	0.53 (0.44)	0.21 (0.31)	7.6	2.4**
Land-use percentage (m^2)	0	7.2–20.3	7.6	3.29**
Nitrate	2.5 (0.3)	3.05 (0.8)	7.6	2.91**
Dissolved oxygen (mg O_2/l)	9.9 (0.2)	8.3 (0.3)	7.6	1.33
pH	8 (0)	8 (0.5)	3.8	1.57

Total inertia was 0.26. Probability (*P*) refers to Monte Carlo test using 999 permutations

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Discussion

Land-use effects

In agreement with the first hypothesis, the findings of this study suggest that human impacts influence the physicochemical characteristics of streams. The higher conductivity of degraded streams was in agreement with Growns & Davis (1991) and Kasangaki et al. (2006) who reported water conductivity to be greater in deforested streams. In addition, the greater nutrient input in degraded areas has been observed by several authors (e.g., Von Schiller et al., 2007). The increase of export of nitrite and nitrate has been observed in predominantly agricultural and urban catchments compared with native forested basins (Osborne & Wiley, 1988; Johnson et al., 1997). Elevated water temperature has been associated with deforestation (Dodds, 2002), and this variable was high in degraded streams. The high temperature of impacted streams was a result of decreased shading and consequent increased solar insolation (Chapman & Chapman, 2003).

In accordance with the second hypothesis, the modifications in environmental characteristics associated with land-use change influenced community structure. Non-degraded streams were characterized by species-rich, diverse, and even communities, whereas simplified degraded stream communities were dominated in abundance by tolerant taxa. The increment in macroinvertebrate abundance in response to land-use change was also observed by other studies of high-gradient streams (Duncan & Brusven, 1985; Stone & Wallace, 1998). In general, environmental perturbation reduces taxa richness to a few tolerant and generalist groups. Considering degraded streams, the contribution of Oligochaeta and Chironomidae was around 71% of total macroinvertebrate abundance during pre-monsoon period. These taxa are considered tolerant and typical of impacted environments (Clements, 1994; Karr & Morishita-Rossano, 2001).

Many studies from both tropical and temperate streams have also found species diversity and richness to decrease in areas that have been impacted by human activities (Stone & Wallace, 1998; Ometo et al., 2000; Benstead et al., 2003). Lower macroinvertebrate diversity could also be associated with the increases in sediment loads expected in degraded streams that decrease habitat heterogeneity (Hynes, 1975; Allan et al., 1997). High bankful erosion was observed in degraded streams of Lules river basin, and this factor was evidence of elevated sedimentation rates in these sites. This was an expected observation given that forest clearance, particularly that of riparian zones, often gives rise to increased soil erosion and subsequent inputs of sediment into streams (Waters, 1995; Harding et al., 1998). Higher sediment loads may occur in degraded streams mainly during storms, particularly during the wettest part of the year (November–April).

In addition, the influence of abiotic changes on community composition was shown by the CCA: a clear separation from communities requiring cold, high dissolved oxygen waters to those tolerant to warm and more lentic conditions was exposed by this ordination. Most aquatic insect taxa are quite sensitive to temperature (Wallace & Anderson, 1996; Hawkins et al., 1997). The preference of *Tricorythodes popayanicus* and *Caenis ludicra* generalist mayflies for degraded streams can be explained by their adaptability to fine substrata, slow currents, low dissolved oxygen values (Hynes, 1970; Dudgeon, 1999; Iwata et al., 2003), and elevated water temperatures (Nolte et al., 1997; Kasangaki et al., 2006). The findings of this study were in agreement with Benstead et al. (2003) in a tropical forest of Madagascar, in that collector gatherers (Caenidae and Trichorythidae) dominated degraded streams. Ephemeropteran taxa such as *Camelobaetidius penai* and coleopteran and dipteran families such as Elmidae, Tipulidae, and Psychodidae preferred well-oxygenated waters of non-degraded streams. According to Brown (1987), elmids usually escape from poor environmental conditions such as low dissolved oxygen. Reliance upon plastron respiration restricts most elmids to water nearly saturated with dissolved oxygen, hence to typically shallow, fast flowing, cool streams (Brown, 1987). Indeed, the potential of Elmidae as bioindicator has been studied in Europe (Richoux & Forestier, 1989; García-Criado & Fernández-Alaez, 1995, 2001), North America (Ode et al., 2005), and South America (Fossati et al., 2001; Von Ellenrieder, 2007). The crane flies (Tipulidae) are shredders and are known to be important in organic matter breakdown in streams. Their absence or occurrence in low numbers at degraded sites may be attributed to a lack of plant material on which they could feed.

Spate effects

In contrast with the third hypothesis, spates affected the abundance and evenness, but did not cause changes in the richness and diversity of macroinvertebrate community. This study found a significant decline in benthic invertebrate abundance 2 months after the peak of spate: macroinvertebrate abundance was approximately three times higher during the prespate period compared with post-spate samples. The trend in invertebrate abundance in Lules river basin was in agreement with studies in other regions around the world, where large reductions in invertebrate abundance following spates (Turcotte & Harper, 1982; McElravy et al., 1989; Matthaei et al., 1997; Jacobsen & Encalada, 1998). The high loss rate in this study (70%) was comparable to those reported after peak of spate in other monsoonal tropical streams (Flecker & Feifarek, 1994; Brewin et al., 2000). Such impacts are typically caused by combinations of high shear stress leading to dislodgement, scouring, and abrasion from high sediment loads and substrate mobilization (Downes et al., 1998; Bond & Downes, 2003). The main mechanisms behind the declines observed in the studied streams are likely to be catastrophic substrate mobilization and continued inputs of sediments from eroding banks during subsequent storms. Increased shear stress from high flows removes invertebrates into the water column and produces a catastrophic drift of individuals. The decrease in the abundance of invertebrates could also lead to an increase in community evenness in post-spate samples. In contrast with other studies (Rosser & Pearson, 1995; Jacobsen & Encalada, 1998) diversity and richness did not show significant seasonal variation. Samples taken in mid-March may reflect a community in a state of recovery from disturbance, as the abundance of most taxa was low whereas richness and diversity were similar to predisturbance samples. The lack of significance in the abundance of *Baetodes huaico* between seasons could be associated with certain behaviour traits that enable rapid re-colonization of disturbed substrata. High mobility of individual taxa while crucial to the process of recolonization may also be an important mechanism for avoiding disturbance (Lake, 1990; Wallace, 1990). The persistence of this taxon in smaller tributaries upstream and subsequent rapid downstream drift and aerial recolonization by adults are important strategies that could ensure its resilience in the streams of Lules river basin (Molineri, 2008). Drift is commonly regarded as the primary source of colonists invading new or denuded habitat patches in most tropical stream systems (Ramírez & Pringle, 2001). This facilitates redistribution of the fauna to patches of habitat newly created during the wet-season spates (Boyero & Bosch, 2002). Another source of potential colonization is possibly the hyporheic zone. The use of the hyporheic zone as a refuge by benthic fauna has been observed in a local study (Fernández & Palacios, 1989), suggesting that refuge-seeking behavior of arthropods could also play an important role in faunal recovery of Lules river basin.

Interaction between disturbances

In contrast to the fourth hypothesis, land use had a greater effect on abundance, richness, diversity, and evenness in comparison with spates: all these community metrics differed significantly between land uses while spates only caused changes in abundance and evenness. The difference in invertebrate richness and Oligochaeta abundance between degraded and non-degraded streams was mostly evident in pre-monsoon period. Throughout low-flow period, fine sediments settle out (Everard, 1996; Wright & Symes, 1999), detritus and nutrients no longer move in surface flow, and wastes and toxic materials are not diluted and exported. As a consequence, physicochemical changes in streams caused by land use were more important in low-flow season, affecting strongly macroinvertebrate composition.

The results of this study suggest that some of the observed taxa can be used as indicators of non-degraded streams, draining native forest, and others can be used as indicators of degraded streams, impacted by the extension of agricultural and cattle lands. These taxa can be used in water-quality evaluation and in monitoring the recovery of streams in the study area.

Acknowledgments Special thanks to Hugo R. Fernández for his support during this study. I am also grateful to Celina Reynaga, Carolina Nieto, Carlos Molineri, Verónica Manzo, Fatima Romero, Eva Tejerina, and Paola Rueda Martín for their assistance in sample identification, and to Martin Sirombra for his valuable comments. I greatly appreciate the reviews of Dr. David Dudgeon, for his thoughtful and constructive suggestions, and three anonymous referees, who greatly improved the focus of this article. This study was supported by Agencia Nacional de Promoción Científica y Tecnológica PICT: 01-12529, the Argentine National Council of Scientific Research (CONICET), and the Research Council UNT 26-G309.

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