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30	Abstract	Macrophytes are common inhabitants of lotic environments and, depending on their morphological traits, possess adaptations that provide shelter to aquatic invertebrates against strong river flow and predators. They may also be used as a food source by macroinvertebrates. The main goal of this study was to determine the relationship between the red alga <i>Paralemanea mexicana</i> and its role as a shelter and/or food source for lotic macroinvertebrates. We also conducted research on the role of microhabitat and morphological variations of the alga in determining macroinvertebrate taxon abundance, diversity, and functional group composition in a high-current velocity river. Results showed that changes in cover and morphology of <i>P. mexicana</i> were mostly correlated with river current velocity, irradiance, and seasonal variation. In turn, these were related to changes in abundance and diversity of the associated macroinvertebrate community. In addition, six macroinvertebrate functional feeding groups were evaluated for associations with the red alga: filtering and gathering collectors, piercers, scrapers, herbivore shredders, and predators. The results showed that the Trichoptera Hydroptilidae genera <i>Ochrotrichia</i> and <i>Metrichia</i> use <i>P. mexicana</i> as a food source and case-building material. The Trichoptera Glossosomatidae <i>Mortonella</i> uses the alga as a substrate. The biotic interactions between <i>P. mexicana</i> and associated macroinvertebrates reveal the importance of macrophytes as purveyors of substrate, as food and shelter for macroinvertebrates, and also as promoters of macroinvertebrate herbivory likely facilitates vegetative propagation of the red alga through increased release and germination of carpospores and new gametophytes.
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#### Associations Between Macroinvertebrates and Paralemanea 4mexicana, an Endemic Freshwater Red Alga from a Mountain River 5in Central Mexico 6

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#### 59Introduction

60 The phenotypic expression of many benthic organisms 61inhabiting lotic environments prevents their dislodgement 62 by the current, either holding a specific spatial position or 63 allowing for movement in the water current (Merritt et al 2008). As such, several adaptations can be noted like the 64 65morphological traits of lotic macrophytes (Cattaneo et al

#### Abstract

Macrophytes are common inhabitants of lotic environments and, depending on their morphological traits, possess adaptations that provide shelter to aquatic invertebrates against strong river flow and predators. They may also be used as a food source by macroinvertebrates. The main goal of this study was to determine the relationship between the red alga Paralemanea mexicana and its role as a shelter and/or food source for lotic macroinvertebrates. We also conducted research on the role of microhabitat and morphological variations of the alga in determining macroinvertebrate taxon abundance, diversity, and functional group composition in a high-current velocity river. Results showed that changes in cover and morphology of *P. mexicana* were mostly correlated with river current velocity, irradiance, and seasonal variation. In turn, these were related to changes in abundance and diversity of the associated macroinvertebrate community. In addition, six macroinvertebrate functional feeding groups were evaluated for associations with the red alga: filtering and gathering collectors, piercers, scrapers, herbivore shredders, and predators. The results showed that the Trichoptera Hydroptilidae genera Ochrotrichia and Metrichia use P. mexicana as a food source and case-building material. The Trichoptera Glossosomatidae Mortonella uses the alga as a substrate. The biotic interactions between P. mexicana and associated macroinvertebrates reveal the importance of macrophytes as purveyors of substrate, as food and shelter for macroinvertebrates, and also as promoters of macroinvertebrate community diversity. In addition, it was shown that macroinvertebrate herbivory likely facilitates vegetative propagation of the red alga through increased release and germination of carpospores and new gametophytes.

1998, Cheruvelil et al 2002, Declerck et al 2011). Likewise,

macroinvertebrates that inhabit this environment possess a

set of adaptations to deal with it, such as a hydrodynamic

body shape, the presence of anchoring structures, as well as

life cycles capable to cope with daily or seasonal environmen-

tal changes (Voshell 2010). Frequently, lotic benthic macro-

invertebrates make use of macrophytes as providers of ref-

uge from the water current, reducing the risk of

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74dislodgement, and as a food source. The latter can be asso-75ciated with habitat selection patterns of macroinvertebrates. 76Other factors, such as water temperature, solar radiation, 77 and substrate composition, also have a direct effect on this 78behavior (Hershey et al 2010, Voshell 2014). The relationship 79between substrate type and the structure and diversity of 80 benthic macroinvertebrate communities is determined in part by the mineral or organic substrate composition or both 81 82 (Dewalt et al 2010, Reid et al 2010). The organic substrate 83 interacts physically and biologically with aquatic macroinver-84 tebrates, while the inorganic substrate interacts physically 85 and chemically with them (Reid et al 2010). In general, pop-86 ulation dynamics of macroinvertebrate communities are re-87 lated to local environmental factors (Cattaneo et al 1998, Cheruvelil et al 2002). Interactions between macrophytic al-88 89 gae populations and macroinvertebrates may be of great 90 importance to promote habitat heterogeneity, resulting in 91 complex relationships between them since macroinverte-92brates spend most of their lives attached to the substrate 93(Dewalt et al 2010).

94Macrophyte communities represent one of the most 95widely distributed and structurally complex organic 96 substrates in rivers. These communities can increase 97habitat heterogeneity by modifying some of the physical traits of lotic ecosystems, such as current velocity, 98substrate composition, and detritus accumulation 99100(Dudley et al 1986, Alonso & Camargo 2010). 101Macrophytes can support filtering and gathering collec-102tor functional groups of macroinvertebrates by slowing 103 the movement of and trapping fine organic and inor-104ganic particles transported in the water current (Dudley 105et al 1986, Walker et al 2013). Some benefits to the 106algae can be perceived as a result of these interac-107tions: greater growth and uptake of more nutrients in 108response to moderate macroinvertebrate herbivory, re-109duction in self-shading from sunlight as a consequence of macroinvertebrates scraping off the top layer of al-110111 gal cells (Dewalt et al 2010, Voshell 2014), and the 112herbivory by grazers that facilitate nutrient regenera-113tion and removal of older, less productive algal tissue 114(Lodge 1991). However, sometimes these interactions can have negative effects; for example, Dudley et al 115116 (1986) observed that algae and sedentary macroinver-117tebrates can compete for space.

118Symbiotic relationships between algae and macroinverte-119brates have been well documented (Hershey et al 2010). For 120example, Nostoc parmelioides Kützing (Cyanobacteria) and 121 Cricotopus nostocicola Wirth (Chironomidae) share a rela-122tionship in which the feeding process of the chironomid 123midge alters the algal colony's morphology, increasing the 124 photosynthetic rate (Ward & Cummins 1978, Dewalt et al 1252010). Another example is the symbiosis between Lemanea 126australis Atkinsion (Rhodophyceae) and Dibusa angata Ross 150

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(Trichoptera), in which the caddisfly uses the red alga as a 127 food and case-building source (Resh & Houp 1986). 128

Lotic freshwater red algae grow under very specific con-129ditions, and in general, they lack adaptations such as resting 130or dispersal cells that would allow them to spread over large 131ranges (Sheath & Hambrook 1990). This can limit their role as 132abundant and frequent taxa in a region (op. cit.). Taking into 133account the empirical evidence described in the literature, 134we assume that when the local environmental conditions 135allow the establishment of any given algae species, it usually 136forms conspicuous and abundant growths and significantly 137contributes to habitat heterogeneity, serving also as a mac-138roinvertebrate food source and/or shelter. 139

The main goal of this study was to determine if a positive 140relationship exists between the morphological traits of the 141endemic red alga Paralemanea mexicana (Kützing) Vis et 142Sheath and the macroinvertebrates that use it for food 143and/or shelter, considering the influence of seasonal varia-144tion. This study was carried out using two measurement 145procedures in a fast-flowing river: (a) microhabitat character-146 ization and morphological variation of the alga and (b) as-147sessment of richness, diversity, and functional groups of 148macroinvertebrates associated with the alga. 149

- Materials and Methods
- Paralemanea mexicana

The genus Paralemanea is characterized by a pseudoparen-152chymatous bambusiform thallus morphology that has a 153multiseriate filament medulla and a pattern of false and true 154branches (Sheath et al 1996a). It has a heteromorphic life 155cycle that includes a visible gametomorphic phase. When 156fertilization occurs, the gametes form a diploid cell that mul-157tiplies to produce carpospores. These carpospores germinate 158into a diploid Chantransia stage, which produces a new ga-159metophyte through somatic meiosis (Carmona & Necchi 1602002). In *P. mexicana*, the gametophyte may be present year 161around and, as such, have abundant populations during win-162ter. The gametophyte also shows structural and reproductive 163changes associated with seasonal variation (Carmona et al 1642014). These traits suggest that the gametophyte is a poten-165tial substrate and food source for benthic macroinverte-166brates (Hambrook & Sheath 1987, Hershey et al 2010, 167Walker et al 2013). Paralemanea mexicana is restricted to 168mountain rivers in Central Mexico with certain microhabitat 169conditions (Carmona & Necchi 2002, Bojorge et al 2010). 170

#### Sample collection

Samples were collected from a segment of the mountainous 172 (1890 m altitude) fifth-order Amanalco River in Central 173

Paralemanea mexicana and Associated Macroinvertebrate Communities

174Mexico (19°13'N, 100°07'W). Fieldwork was conducted from Nov. 2007 to Nov. 2008, which included the most contrast-175ing seasonal environmental cycles (García 2004): the rainy, 176177cool dry, and dry seasons. Three sampling stints were con-178ducted in the dry season: cold early (Dec.), middle (Feb.), and 179warmer end (May). Three more sampling stints were con-180ducted in the middle (Oct. and Nov.) of the rainy season. Five samples were collected during each season, gathered 181 182through an ecological transect. Water temperature and spe-183cific conductance were measured using a Conductronic™ PC-18 conductivity meter (Puebla, Mexico). Discharge ( $Q_3$ , 184 185 $m^3 s^{-1}$ ) was calculated according to Gore (1996). Dissolved 186nutrients were measured by in situ filtering using 0.45- and 1870.22-µm-pore diameter membranes, and later the sample was preserved in chloroform and frozen, in order to avoid 188189bacteriological activity in the water sample. Nutrients were 190measured in the laboratory with a multichannel analyzer, 191following standard titration. Water samples for dissolved in-192organic nitrogen (DIN) and soluble reactive phosphorous (SRP) were kept cold until they were analyzed (APHA 2005). 193

#### 194 Microhabitat characterization

Observations were made on natural boulder substrates di-195rectly on the river bed. Variations over time were monitored 196197 using a quadrat technique (Necchi et al 1995), which evalu-198ates the influence of current velocity, depth, and underwater 199irradiance at the microhabitat level on the vegetative and reproductive characteristics of the algal population. The sam-200201pling site consisted of a 58-m<sup>2</sup> river segment. Each sample 202unit covered a 10-cm radius circle (area = 314.16 cm<sup>2</sup>). The type and size of the sampling units were chosen based on 203204preliminary tests and previous research (Carmona et al 2052006). Sampling consisted of five quadrats, each 2 m apart from the other. Quadrats were positioned within each site on 206207areas with over 5% of alga cover. Their direction and locali-208zation was chosen randomly in an interval between 0° and 209180°. This procedure was repeated along the sampling quad-210rats (in an upstream direction). Microhabitat characteristics 211were recorded on all sampling dates. The microhabitat vari-212ables were measured in situ, approximately in the middle of 213each sampling unit center with five replicates of each sam-214pling unit. Current velocity and irradiance were measured as 215close as possible to the algae using a Swoffer™ 3100 current velocity meter (Seattle, WA, USA) and a LI-COR™ Li-1000 216217quantum meter (Lincoln, NB, USA), with a flat subaquatic sensor of photosynthetically active radiation (PAR), respec-218tively. The variation coefficient (VC) was used to determine 219220whether environmental parameters were consistent (VC = 5-22110%) or variable. Variability in time and space usually results 222from dilution/evaporation processes and biological activity 223 (Magurran 2004). A descriptor for each sample site was

calculated as VC = SE /  $a \times 100$  (SE = standard error and a = 224 mean). 225

#### Paralemanea morphological traits and macroinvertebrate 226 assemblages 227

The number of thallus (gametophytes) within each sampling 228unit was recorded by visual estimation using a 175 cm<sup>2</sup> view-229finder. Twenty-five thalli were randomly selected to measure 230thallus height, number of primary branches, number of 231branches by node, number of true and false branches, num-232ber of Chantransia-stage associates to the gametophyte sur-233face, and number of associated algae species. These charac-234teristics were chosen based on preliminary tests and previ-235ous research (Carmona & Necchi 2002). The numbers and 236taxa of macroinvertebrates were measured for each thallus. 237Macroinvertebrate taxonomy was based on Merritt et al 238(2008), Bueno-Soria (2010), and Thorp & Covich (2010). 239Macroinvertebrate functional groups were assigned accord-240ing to Cummins et al (2005) classification, taking into account 241the characterization of morphological traits that determine 242the food source chosen by macroinvertebrates. Microscopic 243observations were carried out using an Olympus<sup>™</sup> BX51 and 244SZX7 microscopes with DP12 and E-330 microphotography 245systems. 246

#### Data analysis

Species diversity was assessed using the Shannon–Wiener 248diversity test (H log<sub>10</sub>). The Kruskal-Wallis tests were per-249 formed according to the data distribution to assess signifi-250cant differences in environmental and morphological mea-251surements among the six sampling dates. When these tests 252were significant, the Mann-Whitney test was conducted 253among all dates to detect which differed significantly 254 $(P \leq 0.05)$ . Associations between morphometric and repro-255ductive data, microhabitat variables, and total abundance 256of macroinvertebrate taxa during the six sampling dates were 257assessed using Spearman correlation coefficient (Gotelli & 258Elison 2004). The analyses were conducted using SPSS 18 259software (Levesque 2006). We selected the microhabitat pa-260rameters and the algae's morphological traits based on 261Spearman correlation coefficient and the principal compo-262nent analyses (PCA) ( $P \le 0.05$ ) in order to choose the most 263significant variables. Relationships between temporal mor-264phological traits of P. mexicana and macroinvertebrate-265associated taxa and physical parameters were explored 266through a canonical correspondence analysis (CCA), followed 267by Monte Carlo tests (999 permutations,  $P \le 0.05$ ). These 268 analyses were performed using XLSTAT software (Addinsoft 2692702013).

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#### 271 Results

### 272 Environmental characteristics and morphological traits273 of P. mexicana

274During the six sampling periods carried out in a year, the river 275water showed relatively low ion content, near-neutral pH, mild temperatures, and high dissolved oxygen content 276277(Table 1). These physical characteristics were consistent dur-278ing all sampling periods (VC<10%). The rest of the physical 279and chemical variables, such as specific conductance, dis-280charge, SRP, and DIN, exhibited larger variations (VC=51-28165%) with increased values observed during cool and warm dry seasons. Gametophytes occurred predominantly under 282microhabitat conditions of fast current velocity (minimum 283284and maximum = 69–156 cm  $s^{-1}$ ), low-to-medium irradiance 285(minimum and maximum = 13–744  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>), 286and shallow depth (minimum and maximum = 11-20 cm) 287and on boulders as a substrate (Table 1). The Kruskal-Wallis 288test showed significant differences between current velocity (H=12; P=0.04) and irradiance (H=24; P=0.00) among 289290sampling dates.

Gametophytes were present throughout the seasons and covered a mean of 7.4–34% of the thallus. Significant differences in abundance were observed (H=15; P=0.01). The highest percentage coverage of gametophytes on boulders occurred in the cool dry season, and the lowest was in the rainy season (Table 2). There were significant differences

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among sampling dates for all P. mexicana-evaluated morpho-297logical traits (Fig 1). Thallus height changed significantly 298throughout the study (U = 92-210, P = 0.000-0.045). The 299greatest thallus heights were recorded during the cool dry 300 season, and the shortest were observed in the rainy season. 301 Significant differences were observed in the true and false 302branches between seasons (U = 122 - 202; P = 0.001 - 0.024). 303 The number of first-order and true branches was significantly 304 greater during two of the three rainy seasons than in the dry 305 season (U=146-203; P=0.001-0.028). The dry season ex-306hibited more false and whorled branches compared to the 307 rainy and cool dry seasons (U = 122 - 198; P = 0.000 - 0.021). 308

#### Macroinvertebrate richness, diversity, and functional groups 309

Paralemanea mexicana was associated with abundant 310aquatic larvae and pupae. Eleven taxa of macroinverte-311brates found in the sampling sites showed low diversity 312values during all seasons (Table 2). In terms of total 313abundance, the largest density of macroinvertebrates 314was recorded in the dry season. The Orthocladiinae 315chironomid subfamily was found almost exclusively in 316the dry season. In contrast, the Tanypodinae chirono-317mid subfamily was at peak abundance just prior to and 318 throughout the rainy season. Two micro-caddisfly gen-319era of the family Hydroptilidae, Ochrotrichia and 320 Metrichia, were found, but they were less abundant 321than the chironomid midges. These caddisfly larvae 322

t1.2		Rainy (27 Oct. 2007)	Cool dry (5 Dec. 2007)	Cool dry (8 Feb. 2008)	Dry (8 May 2008)	Rainy (3 Sep. 2008)	Rainy (20 Nov. 2008)	Variation coefficient (%) <sup>a</sup>
t1.3	Temperature (°C)	16	14	15	18	17	14	10
t1.4	рН	6.8	7.5	8	7	6.7	7.3	6
t1.5	K <sub>25</sub> (μs cm <sup>-1</sup> )	175	197	248	244	165	168	19
t1.6	$Q_3 (m^3 s^{-1})$	3.5	2.9	2.3	2.6	2.9	2.3	16
t1.7	Dissolved oxygen saturation (%)	100	97	94	91	92	93	4
t1.8	SRP	0.82	0.84	0.58	0.66	0.1	0.1	65
t1.9	DIN	2.10	0.53	2.76	1.0	1.27	1.7	51
t1.10	CV (cm s <sup>-1</sup> )	89±21	94±65	70±38	69±.33	132 ± 39	156 ± 69	
t1.11	Irradiance ( $\mu$ mol photons m <sup>-2</sup> s <sup>-1</sup> )	14±5.4	40±6.5	347±428	744 ± 125	256 ± 86	13 ± 2.3	
t1.12	Depth (cm)	11±10.5	17 ± 5.5	19 ± 11.5	20±4	15±8	19 ± 7.5	
t1.13	Number and type <sup>b</sup> of associated algae species	0.6±0.5 Pl, Sc	0.8±0.5 Pl, Oe, St	1.0 ± 0.3 Pl, Sc, Ch, St, M	2.3 ± 0.9 Pl, Sc, Ch, Oe, Cl, Va, M,	0.3±0.6 Pl, Sc	1.3 ± 0.5 Pl, Sc, Oe, Cl,	

t1.1 Table 1 Physical and chemical characteristics of the Amanalco River.

Values are given in milligrams per liter except where indicated.  $K_{25}$  = specific conductivity,  $Q_3$  = discharge.

SRP soluble reactive phosphorous, DIN dissolved inorganic nitrogen, CV current velocity.

<sup>a</sup> Magurran (2004): conservative (VC < 10%) and not conservative (VC > 10%) variables (mean  $\pm$  1 SE; n = 25).

<sup>b</sup> Cyanobacteria: *Placoma* sp. (Pl); Rhodophyta: *Sirodotia suecica* Kylin (Ss) and *Chantransia* stage (Ch); Chlorophyta: *Oedogonium* sp. (Oe), *Stigeoclonium* sp. (St), and *Cladophora* sp. (Cl); Heterokontophyta: *Vaucheria* sp. (Va) and mosses (M).

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t2.1 Table 2 Total abundance, richness, diversity, and functional feeding groups of macroinvertebrate taxa associated to *Paralemanea mexicana* in the Amanalco River.

t2.2		Rainy (27 Oct. 2007)	Cool dry (5 Dec. 2007)	Cool dry (8 Feb. 2008)	Dry (8 May 2008)	Rainy (3 Sep. 2008)	Rainy (20 Nov. 2008)
t2.3 Taxa and functional groups in the sample (total abundance of individuals per group)		Tanypodinae- P(26) Simulium-FC(16) Ochrotrichia- PC(2) Metrichia-PC(2) Lara-DSH(2) Orthocladiinae- GC(1) Baetis-GC(1) Mortoniella- SC(1)	Orthocladiinae- GC(179) <i>Metrichia</i> -PC(19) <i>Simulium</i> -FC(16) Acari-GC/PC(1) <i>Ochrotrichia</i> -PC(1)	Orthocladiinae- GC(187) <i>Mortoniella</i> -SC(9) <i>Metrichia</i> -PC(7) <i>Ochrotrichia</i> -PC(6) <i>Lara</i> -DSH(3) Acari-GC/PC(1)	Orthocladiinae- GC(340) Tanypodinae-P(111) Ochrotrichia- PC(96) Mortoniella-SC(89) Metrichia-PC(42) Acari-GC/PC(5) Simulium-FC(5) Lara-DSH(3) Baetis-GC(2) Cleptelmis-HSH(1) Phanocerus-HSH(1)	Tanypodinae- P(93) <i>Metrichia</i> - PC(12) Orthocladiinae- GC(4) <i>Mortoniella</i> - SC(2) <i>Simulium</i> -FC(2) <i>Phanocerus</i> - HSH(1)	Tanypodinae- P(293) Orthocladiinae- GC(20) Simulium- FC(20) Ochrotrichia- PC(4) Metrichia-PC(1) Acari-GC/PC(1) Baetis-GC(1)
t2.4	Dominance of macroinvertebrate taxa and functional feeding group	Tanypodinae (P)	Orthocladiinae (GC)	Orthocladiinae (GC)	Orthocladiinae (GC)	Tanypodinae (P)	Tanypodinae (P)
t2.5	Total abundance	51	216	213	695	114	340
t2.6	Taxa diversity (Shannon– Wiener Index)	0.44	0.23	0.16	0.43	0.24	0.2

Functional feeding groups follows the Cummins *et al* (2005) classification: gatherers–collectors (GC), piercer (PC), scrapers (SC), filterers–collectors (FC), predators (P), and herbivores–shredders (HSH).



Fig 1 Morphological traits measured for seasonal samples of *Paralemanea mexicana* in the Amanalco River: *a* algal cover (%), *b* thallus height (cm), *c* first-order branch, *d* true branches, *e* whorled branches, *f* false branches, *g* epiphytic Chantransia stages, and *h* associated algae species. Sampling dates indicated with the *same letter* do not significantly differ (Mann–Whitney test, mean  $\pm$  1 SE; *n* = 25).

are specialized to feed by piercing algal cells and sucking out the contents. The greatest micro-caddisfly
abundance was during the dry season. All the taxa
identified were found at every sampling station with
the exception of the riffle beetle *Phanocerus*(Elmidae) for which only one individual was collected.

329The diversity index values, in general, were low, between 0.44 and 0.16, and do not show a strong rela-330 331tionship with seasonal variation. The highest values 332correspond to the Oct. 2007 rainy season with a total 333abundance of 51 organisms belonging to eight taxa and 334 to the May 2008 dry season with a total abundance of 335695 organisms belonging to 11 taxa. Conversely, the 336lowest values correspond to the Feb. 2008 cool dry 337 season represented by six taxa, but most of the sam-338ples was dominated by organisms belonging to 339Orthocladiinae subfamily. The other two rainy seasons 340(Sep. and Nov. 2008) were represented by five and six 341 taxa, respectively, and dominated by the Orthocladiinae 342 subfamily as well (Table 2).

343Some macroinvertebrates that have specific feeding 344habits can find an optimal habitat in P. mexicana. For 345example, the piercer caddisfly genera Ochrotrichia and 346Metrichia as well as the Orthocladiinae chironomid subfamily larvae that were found adhered to thallus surface 347of the alga. The greatest abundance of the caddisflies 348349was associated with the highest density of associated 350moss. The presence of moss correlated with silk cases 351built by the caddisflies by weaving it together with 352P. mexicana and diatoms. Metrichia's cases were found 353attached to the alga thallus in a dorsal-ventral position, 354similar to that observed for the Glossosomatidae caddisfly genus Mortoniella. The cases of Orchrotrichia 355356were found adhered to the algal thallus hanging from a 357 peduncle. When observed under a microscope, the cases had more than one peduncle even if they were 358only attached to the thallus by a single one. The forma-359360 tion of refuges did not represent the predominant form 361of the algal or plant tissue. The Orthocladiinae chirono-362mids built cases adhered to P. mexicana with some also 363found within Sirodotia suecica filaments. Black flies in the genus Simulium were frequently found in the sam-364365ples but were few in numbers. Genera of the Elmidae 366beetle family were rare, mostly represented by the 367 xylophage (wood-eating) genus Lara.

368The specific traits observed for the algal substrate were 369related to the different macroinvertebrate functional feeding 370groups (FFGs) identified in this study. Four dominant FFGs 371were found in the samples. In the order of the highest abun-372dance, these were gatherers-collectors, predators, piercers, 373 and filterers-collectors. Piercers, represented by two micro-374trichopteran genera, were abundant during the dry season 375and absent during the rainy season.

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Red algal morphological traits and macroinvertebrate assemblages

Some significant correlations were found between algal mor-378 phological traits, microhabitat conditions, and macroinverte-379 brate taxa (Table 3). During the rainy season, the taxa posi-380tively correlated with P. mexicana morphological traits were 381*Metrichia* with algal cover ( $\rho = 0.894$ ), *Simulium* with thallus 382height ( $\rho = 0.894$ ), and Tanypodinae with associated algae 383 species ( $\rho = 0.90$ ). Negative correlations were found be-384tween Simulium and first-order and false branches of the 385alga as well as associated algae species ( $\rho = -0.894$ ) and with 386 Tanypodinae ( $\rho = -0.90$ ). During the dry season, the positive 387 correlations between macroinvertebrate taxa and algal mor-388phological traits were first-order branches with Metrichia 389  $(\rho = 0.947)$  and thallus height with *Mortoniella*  $(\rho = 0.894)$ . 390A negative correlation was found between algal whorled 391branch pattern and the genera Mortoniella and 392 Ochrotrichia ( $\rho = -0.90$  for both correlations). During the 393 rainy season, Orthocladiinae and Ochrotrichia were found 394to be positively correlated ( $\rho = 1.00$ ), but Tanypodinae and 395Simulium were negatively correlated ( $\rho = -0.889$ ). 396

The total variances in the PCA explained the 90% of 397 total variation in the first two axes. The first axis (78%) 398was corresponded to true branches, associated algae 399species, and the number of whorled branches. The sec-400 ond axis (12%) was represented by the thallus height, 401 false branches, and the number of Chantransia stages. 402 According to the CCA test (Fig 2), irradiance and current 403velocity had a significant influence on the abundance of 404the associated macroinvertebrates, where 99% of the 405total variation was explained by the first two axes 406  $(P \le 0.05)$ . The first axis (88%) shows a positive relation-407 ship between irradiance (0.916), total abundance of mac-408roinvertebrates (0.314), and the number of associated 409algae species (0.257), in the cool dry (0.636) and dry 410(1.389) seasons. The second axis (11%) was positively as-411 sociated with current velocity (0.407) in the two rainy 412seasons (0.826 and 0.677, respectively). 413

#### Discussion

We found that the thallus of *P. mexicana* favors microhabitat 415conditions typical of mountain rivers with low incident radi-416 ation, firm substrates, and high-speed current velocities. 417 These traits are related to a series of morphological adapta-418 tions that are specific of algal species that thrive in rivers with 419the highest current velocities an alga can tolerate (Sheath & 420 Hambrook 1990). A ridged thallus, multiple aggregated ga-421 metophytes that develop from a rhizoidal system, and a 422wide-branching pattern throughout the thallus (Carmona 423 et al 2014) make P. mexicana a stable habitat for 424

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t3.1 Table 3 Spearman correlation coefficient between the morphological traits of *Paralemanea mexicana*, microhabitat variables, and macroinvertebrate taxa in the Amanalco River.

t3.2	Variable	Таха	Rainy (27 Oct. 2007)	Cool dry (5 Dec. 2007)	Cool dry (8 Feb. 2008)	Dry (8 May 2008)	Rainy (3 Sep. 2008)	Rainy (20 Nov. 2008)
t3.3	Current velocity (cm s <sup>-1</sup> )	Orthocladiinae	·	·	-0.9			
t3.4		Tanypodinae						-0.975 <sup>ª</sup>
t3.5	Irradiance ( $\mu$ mol photons m <sup>-2</sup> s <sup>-1</sup> )	Orthocladiinae		0.9 <sup>ª</sup>				
t3.6		Simulium						0.894ª
t3.7		Tanypodinae						-0.9 <sup>ª</sup>
t3.8	Algal cover (%)	Tanypodinae	–0.918 <sup>a</sup>					
t3.9		Metrichia					0.894ª	
t3.10	Total abundance of	Orthocladiinae			0.9 <sup>ª</sup>			
t3.11	macroinvertebrates	Metrichia					-0.918 <sup>ª</sup>	
t3.12		Tanypodinae						1 <sup>b</sup>
t3.13	Seasonally	Orthocladiinae			0.9 <sup>ª</sup>			
t3.14		Mortoniella				0.9 <sup>a</sup>		
t3.15		Tanypodinae						-1 <sup>b</sup>
t3.16	Thallus height	Mortoniella			0.894 <sup>ª</sup>			
t3.17		Simulium			$\mathbf{O}$			0.894 <sup>ª</sup>
t3.18	First-order branches	Metrichia				0.947 <sup>ª</sup>		
t3.19		Simulium						-0.894 <sup>ª</sup>
t3.20	Whorled branches	Mortoniella				-0.9 <sup>ª</sup>		
t3.21		Ochrotrichia				-0.9 <sup>ª</sup>		
t3.22		Tanypodinae						0.975 <sup>ª</sup>
t3.23	False branches	Simulium						-0.894 <sup>ª</sup>
t3.24		Tanypodinae						-0.9 <sup>ª</sup>
t3.25	Associated algae species	Simulium				1 <sup>b</sup>	-0.889ª	
t3.26		Orthocladiinae					-0.892 <sup>a</sup>	
t3.27		Tanypodinae						0.9 <sup>ª</sup>
t3.28	Orthocladiinae	Ochrotrichia	1 <sup>b</sup>					
t3.29	Tanypodinae	Simulium					-0.889 <sup>ª</sup>	

<sup>a</sup> Correlation is significant at the 0.05 level.

<sup>b</sup> Correlation is significant at the 0.001 level.

macroinvertebrates and other algae. Therefore, *P. mexicana*increases the habitat heterogeneity of a river segment where
it grows and can have a significant effect on the distribution
of local macroinvertebrate and algal taxa.

429Seasonal changes in the abundance and branching pattern 430of this red alga were related to habitat preferences of macro-431 invertebrates, predominantly caddisflies and chironomid 432midges, as reported in similar previous studies (Resh & Houp 4331986, Sheath et al 1996b, Carmona et al 2009). The drag and damage that current velocity can cause to macroinvertebrates 434435likely leads to evolutionary adaptations in body shape as well as feeding and movement patterns (Hershey et al 2010). In 436fact, hydrodynamic forces interact strongly with substrate 437438type in modeling habitat conditions, and at the local scale, they 439represent the most important factors in determining the type 440 and abundance of macroinvertebrates (Dewalt et al 2010). 441 Therefore, the protective morphology of P. mexicana makes

it a highly desirable substrate, offering shelter from the phys-442ical effects of high riverine current velocities.443

Oligotrophic-to-eutrophic conditions were recorded year 444around in the Amanalco River (according to Dodds 2003: DIN 445 0.02–2 mg  $L^{-1}$  and SRP 0.2–0.8 mg  $L^{-1}$ ). Changes in DIN were 446 highly variable, probably due to upstream agricultural water 447withdrawals and releases. According to Vannote et al (1980) 448 and Bowman et al (2005), moderate nutrient enrichment and 449light input can increase the abundance of algae and macroin-450vertebrates in a river. However, when nutrient enrichment is 451excessive, the opposite effect can happen and the abundance 452of sensitive organism decreases (Merritt et al 2008). The effect 453of moderate nutrient enrichment was confirmed in this study 454during different seasons. For example, the DIN showed an 455increase from 0.5 mg  $L^{-1}$  in the cool dry season to 2 mg  $L^{-1}$  in 456 the rainy season, and the highest macroinvertebrate diversity 457(0.44) was associated with intermediate values of DIN; when 458 459 nitrogen concentrations were lowest (0.5 mg  $L^{-1}$ ) and highest 460 (3 mg  $L^{-1}$ ), the macroinvertebrate diversity decreased to al-461 most half (0.23 and 0.16, respectively).

462 In the cool and dry seasons, gatherers-collectors and 463scrapers were the dominant macroinvertebrates. In the wet 464 season, a significant portion of filterers-collectors and preda-465 tors were observed, probably because an algal and prey food source became available. It is not uncommon to observe an 466 467 increase in the abundance of filterer-collector macroinverte-468brates in lotic environments (Merritt et al 2008). Paralemanea 469 mexicana abundance was also related to a possible preference 470 of micro-caddisflies for this alga when the number of its first-471 order and whorled branches increased. The latter could be 472explained due to the presence of these branches in the outer 473cortex which is less thick/packed than the inner cortex. 474 Additionally, the juvenile branches in the P. mexicana thallus 475are less corticated than the older branches (Carmona & Necchi 476 2002), which could favor the perforation of the thallus by 477 piercing macroinvertebrates (Lodge 1991).

478The CCA results shows that a significant positive correla-479 tion exists between the branch arrangement and the number 480 of associated algae species (including Cyanobacteria, Chlorophyceae, and other red algae) that could explain the 481482higher occurrence and abundance of macroinvertebrates. 483 Thallus that is more branched becomes a richer food source and diversity of microhabitats that support macroinverte-484485brate assemblages (Walker et al 2013). On the other hand, 486 high irradiance values proved to be a unique microhabitat

parameter allowing the highest growth in some algae groups487during the dry and cool seasons. In fact, during these sea-488sons, the diversity and abundance of microinvertebrates with489piercing-herbivore feeding preferences was the highest, as490well as for the Hydroptilidae family which is reported in as-491sociation with algae nearly always (Alonso & Camargo 2010).492

The presence of P. mexicana and particularly the differ-493ences in its morphological traits provide supporting evidence 494of its role as a facilitator of diverse macroinvertebrate com-495munities and associated algae by providing refuge and nutri-496tional sources, under stressful environmental conditions such 497as those of high-current velocity rivers (Alonso & Camargo 4982010, Walker et al 2013). The CCA results were concordant 499with the positive Spearman correlations between the red 500algae and certain macroinvertebrates, mostly micro-501caddisflies. In particular, thallus height and first-order 502branches encourage the settlement of macroinvertebrates 503that build portable cases. The negative correlations of red 504 algal false branches with the presence of Mortoniella and 505Ochrotrichia could be related to the reduced moving capa-506bilities of the larvae along the thallus. 507

The results show that the largest extensions of habitat 508 coverage by *P. mexicana* were observed during the cool dry 509 season (34%) and the dry season (19%). Also, the greatest 510 richness and diversity of macroinvertebrates was recorded 511 during the dry season (11 taxa, H' = 0.44). As such, these results show that excessive algal habitat cover does not necessarily increase the diversity and abundance of associated 514



Fig 2 Canonical correspondence analysis biplot of the general distribution of morphological traits of *Paralemanea mexicana* (star symbols) and the total abundance of macroinvertebrates with regard to microhabitat variables (*circle symbols*) recorded in the climatic seasons (*rhombus symbols*).

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macroinvertebrates, in contrast with other studies (Alonso & 515Camargo 2010, Walker et al 2013). For example, some taxa 516that feed by scraping rock surfaces or adhere to them, like 517518Simulium, are inhibited by filamentous and mucilaginous al-519gae, which may be an indication of competition for space 520(Dudley et al 1986). Thus, an increase in P. mexicana habitat 521cover could limit the abundance of some macroinvertebrates that do not rely on the red alga as a source of food or shelter. 522523In contrast, the greatest abundance of the predaceous 524Tanypodinae midges was found during the rainy season in 525combination with reduced red algal habitat cover, suggesting 526that other interactions may occur, such as active predation, 527since some tanypod species are known to prey on other 528macroinvertebrates (Merritt et al 2008).

529Ruptures in the thallus and a larger number of false 530branches and filamentous structures of the Chantransia 531stage could have been due to the presence of the 532Metrichia and Ochrotrichia hydroptilid caddisflies, owing to 533increased habitat heterogeneity (Walker et al 2013). These genera use fragments of the red alga for case building, similar 534to other caddisflies with the red alga Lemanea (Resh & Houp 5355361986). Although the caddisflies' behavior damages the game-537tophyte structure, it proves beneficial to the alga because it favors the release and germination of the carpospores, giving 538way to the next stages in the alga's life cycle (Carmona et al 5392014). The increase in filaments of the Chantransia stage and 540541thallus of the red alga S. suecica might also be an important 542energy source for macroinvertebrate herbivores (Hambrook 543& Sheath 1987).

The presence of more than one peduncle on Ochrotrichia 544545cases is probably related to different pupation sites along the red algal thallus (Resh & Houp 1986). This trait was also 546547observed in Mortoniella cases (which were mostly empty). 548It might be explained as the result of a search for better 549environmental conditions, since Mortoniella does not tolerate poor-water quality well (Bueno-Soria 2010), or they could 550represent pupal cases from which adults had emerged. 551552Ochrotrichia and Metrichia build portable cases up until the 553fifth instar, which means the red alga promotes larval growth 554to pupation and adult stages. The greatest abundance of these genera was during the warm dry season, which is their 555adult emergence period (Bueno-Soria 2010). 556

#### 557 Conclusion

558 Seasonal and environmentally induced changes in habitat 559 cover and morphological traits of *P. mexicana* were related 560 to river current velocity, irradiance, and nutrient concentra-561 tions. These in turn were associated with richness and abun-562 dance, case building, and feeding habits of 11 benthic macro-563 invertebrate taxa.

The red alga *P. mexicana* displayed a strong structural 564design, well adapted to withstand the forces of strong river 565current. A perennial population is promoting local micro-566environmental heterogeneity, providing a suitable substrate 567for macroinvertebrates, and supplying shelter and feeding 568grounds. Likewise, it was linked to the provision of shelter 569and materials for the construction of portable cases of the 570hydroptilid caddisfly genera of piercers, Ochrotrichia and 571Metrichia. A similar relationship between P. mexicana and 572the scraper caddisfly Mortoniella was observed in which 573the red alga serves as shelter and provides case material. 574These relationships were apparent because every case was 575found adhered to the red alga thallus attached by specialized 576structures such as peduncles. 577

The effects of herbivory on *P. mexicana*'s thallus were 578apparently beneficial for the alga by promoting the release 579and germination of carpospores. The main type of herbivory 580to which the alga was subject was consumption of cellular 581contents rather than structural tissue. However, the algal 582cover by *P. mexicana* plays a significant role in the establish-583ment of the macroinvertebrate community. An excessive al-584gal growth might promote competition for substrate by the 585colonization of sedentary species of macroinvertebrates that 586 adhere to rock surfaces, but it would also favor species asso-587 ciated with the alga thallus. This study contributes providing 588evidence on interactions in aquatic ecosystems, which are 589rarely documented, but are important because the species 590or taxa groups involved could be exerting great effects on the 591structure and productivity of benthic organisms. 592

Interspecific facilitation is an ecological mechanism that 593can promote the efficiency of resource use and persistence 594in stressful conditions in P. mexicana and its associated mac-595roinvertebrate assemblages. Nevertheless, these associa-596tions may not have been as common in the study area be-597cause it is restricted to an isolated geographic region with 598particular microhabitat conditions. The latter suggests that 599special morphological traits and interactions promote evolu-600 tionary adaptations to successfully compete with other lotic 601 macrophytic species in similar tropical mountain rivers. 602

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- "Voshell 2010" is cited in text but not given in the reference list. Please provide details in the list or Q1. delete the citation from the text.
- Q2. Occurrences of the term "algal associated species" were changed to "associated algae species" to ensure consistency throughout the manuscript. With this regard, please consider changing the term "algal associated species" found in the artwork of Figures 1 and 2 to "associated algae species".

nd 2 to "c