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Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands

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1 **Scale dependency of processes structuring metacommunities of**
2 **cladocerans in temporary pools of High-Andes wetlands.**

3

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15 **Abstract**

16 Metacommunity structure can be shaped by a variety of processes operating at different
17 spatial scales. With increasing scale, the compositional variation among local
18 communities (beta diversity) may reflect stronger environmental heterogeneity, but may
19 also reflect reduced exchange of organisms between habitat patches. We analyzed the
20 spatial architecture of a metacommunity of cladoceran zooplankton in temporary pools of
21 High Andes wetlands, with the objective of explaining the spatial dependency of its
22 structure. The spatial distribution of the pools is hierarchical and highly discontinuous:
23 pools are clustered within small wetlands, which lay scattered over valleys that are
24 separated from each other by mountain ridges. We studied a total of 59 pools, belonging
25 to six different wetlands in four different valleys. We assessed pool environmental
26 heterogeneity and sampled active communities and dormant propagule banks of
27 cladoceran zooplankton. Environmental heterogeneity proved very high within wetlands
28 and showed almost no increase with increasing spatial scale. Conversely, diversity
29 partitioning analyses indicated an increase in beta diversity with spatial scale, especially
30 among valleys. Variation partitioning on environmental data and spatial RDA models
31 suggested environmental heterogeneity as the most important generator of beta diversity
32 within wetlands. At the largest spatial scale, beta diversity manifested itself mainly as a
33 differentiation of species occurrence patterns among valleys, which could not be entirely
34 explained by environmental variables. Our study thus presents a case where
35 environmental control seems to be the dominant metacommunity structuring process at
36 the smallest spatial scale, whereas neutral processes and dispersal limitation are the most
37 likely generators of beta diversity at the largest spatial scale.

38 **Introduction**

39

40 The importance of spatial scale has increasingly been recognized in community ecology,
41 especially during the latest decades (Menge and Olson 1990). Compositional variation
42 among communities (beta diversity) can be generated by different factors and the relative
43 importance of these factors can vary among spatial scales. One important reason for this
44 is that environmental variables that shape communities may differ in their range of
45 variation among spatial scales. Some variables show large variation at small spatial scales
46 and will therefore generate high community dissimilarity in relatively small areas. Other
47 important variables only show substantial variation at large spatial scales, and will thus
48 only give rise to community variation in large study areas (Borcard et al. 2004).

49 A second major driver of beta diversity is dispersal limitation. Since the
50 breakthrough of the metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005),
51 community ecology has increasingly considered alternative models of spatial dynamics in
52 explaining patterns of diversity within and among communities at the landscape scale.
53 Dispersal plays a pivotal albeit different role in all these models. Neutral and patch
54 dynamics models, which assume absence of species interactions with the environment
55 (Hubbell 2001), strongly rely on dispersal limitation to explain patterns of (meta-)
56 community structure. Conversely, the species sorting model (sensu Leibold et al. 2004,
57 Cottenie 2005, also referred to here as ‘environmental control’) explains community
58 composition by the interaction of species niches with the abiotic and biotic environment
59 and assumes that dispersal limitation does not prevent species from tracking
60 environmental gradients in space and time. In the case of mass effects, massive fluxes of

61 individuals from source to sink communities can overwhelm the effect of local conditions
62 and species interactions (Vanschoenwinkel et al. 2007, Guelat et al. 2008). The potential
63 of organisms to disperse among habitat patches within metacommunities depends on the
64 distance and type of connections among patches (Shurin et al. 2009). As spatial scale is
65 intrinsically related to the among-patch distances and the physical structure of the
66 landscape, it is expected to be very important in determining the type and strength of
67 alternative types of spatial dynamics that shape metacommunity structure (Dumbrell et al.
68 2008).

69 The revival of diversity partitioning techniques (Lande 1996, Veech et al. 2002,
70 Jost 2007) has strongly enhanced research on the spatial organization of biodiversity in
71 metacommunities. For spatially nested datasets, these techniques allow researchers to
72 decompose overall gamma diversity (total regional diversity) into alpha diversity (mean
73 local diversity) and components of beta diversity for each level of spatial scale. Although
74 this approach has considerably increased our knowledge on the overall architecture of
75 metacommunity biodiversity for several organism groups in a variety of landscape
76 contexts (Stendera and Johnson 2005, Diekötter et al. 2008, Lindo and Winchester 2008),
77 it often has limited power in explaining the observed patterns when standing on its own.
78 Parallel to the development of diversity partitioning, an increasing number of studies
79 have tried to link patterns of community variation with existing metacommunity
80 paradigms (Holyoak et al. 2005) by partitioning community variation into spatial and
81 environmental components (Borcard et al. 1992, Cottenie 2005), using direct gradient
82 ordination techniques (Legendre et al. 2005). These studies have increased our
83 understanding of processes underlying metacommunity patterns, but the large majority of

84 these studies are confined to a single spatial scale. In order to get a better understanding
85 of the link between the structure and dynamics of metacommunities at different levels of
86 spatial scale, there is a need for an integrated approach through the combined application
87 of these two analytical frameworks.

88 Due to their discontinuous distribution at multiple spatial scales, temporary pools
89 of small wetland systems in the high Andes provide an interesting model system for the
90 study of scale dependency in aquatic invertebrate metacommunities. The spatial
91 distribution of pools in this part of the Andes is hierarchical: pools are clustered within
92 small wetlands and are to a variable degree connected with each other during periods of
93 high rainfall. These wetlands lay scattered over valleys that are separated from each other
94 by mountain ridges with height of approximately 450 m. For this study, we focused on
95 cladoceran zooplankton, a group of passively dispersing aquatic invertebrates (Bohonak
96 and Jenkins 2003) for which time-integrated species lists of individual pools can readily
97 be obtained through the analysis of dormant propagule banks (Vandekerkhove et al.
98 2005a, 2005b). We sampled pools at three levels of spatial scale (i.e., within-wetlands,
99 within valleys and among valleys) with the aim of dissecting the spatial architecture of
100 the metacommunity and evaluating the relative importance of alternative metacommunity
101 processes for each level of spatial scale. We expected beta diversity among pool
102 communities to increase with increasing spatial scale and set out to explore if that
103 increase corresponded to community patterns that should emerge from stronger
104 environmental control along more pronounced environmental gradients, or whether these
105 patterns were more consistent with the patterns that were expected to emerge as a result
106 of stronger dispersal limitation. At the smallest spatial scale, the scale of individual

107 wetlands, we expect little dispersal limitation, given the small size of the wetlands and
108 short distances among pools; conversely, flooding events may lead to homogenization of
109 communities through mass effects. At the intermediate and largest spatial scales, we
110 expect an increase in the importance of dispersal limitation, given the larger among-patch
111 distances, lower hydrological connectivity and the presence of mountain ridges between
112 valleys. In addition, broader environmental gradients may potentially enhance beta
113 diversity at these larger scales, as long as environmental control is not impeded by
114 dispersal limitation (Leibold and Norberg 2004).

115

116

117 **Material and methods**

118

119 **Study area**

120

121 Our study area is located in the Tunari mountain range (Cordillera del Tunari, between
122 17° 19' 19'' and 17° 10' 56'' South latitude and 66° 08' 53'' and 66° 22' 43'' West
123 longitude), at altitudes between 4000 and 4400 m, and is part of the eastern Andes
124 mountain range (Figure 1). It is a mountainous area, with numerous small wetlands
125 (locally called 'bofedales') that lay scattered over the valleys and mountain slopes
126 (Coronel et al. 2004). Most of the wetlands in this area contain small temporary fishless
127 pools, of which the total number typically varies between one and eight, although pools
128 can be more numerous in some of the larger wetlands. The region is subject to a rainy
129 season from October to March and a dry season from April to September. During the

130 latter period, the pools fall dry. We refer to Coronel et al. (2004) for a more detailed
131 description of the limnological features of the pools.

132

133

134 **Sampling design**

135

136 We sampled a total of 59 pools in four different valleys of the Tunari mountain range,
137 i.e., Taquiña, Toro, Saito and San Ignacio. The aim of our sampling design was to study
138 cladoceran community variation at three levels of spatial scale, i.e. at the level of
139 individual wetlands, individual valleys and multiple valleys. Full hierarchical sampling
140 would have required us to sample all pools in the entire set of wetlands in each of the
141 studied valleys, an effort that was unfeasible in the context of the present study. We
142 therefore applied a different approach still allowing us to capture variation among
143 communities at the three levels of spatial scale. For this, we collected two sets of samples
144 (Figure 1). For a first dataset (further referred to as the WTL dataset), we sampled all
145 pools in 6 different wetlands, i.e. two wetlands in Taquiña (Tq1, with 6 pools and Tq2,
146 with 7 pools), two wetlands in Toro (Tr1, with 6 pools and Tr 2, with 5 pools), one
147 wetland in Saito (S1, with 5 pools) and one wetland in San Ignacio (SI1, with 6 pools).
148 The total number of pools sampled for the WTL dataset thus equals 35 from 6 wetlands
149 (Figure 1). For the second dataset (the VALLEY dataset), we selected a number of
150 wetlands in each of the four valleys (13 wetlands in Taquina, 7 in Toro, 5 in Saito and 4
151 in San Ignacio) and in each of these wetlands we sampled one haphazardly chosen pool
152 (Figure 1), including one randomly selected pool of each wetland from the WTL dataset.

153 In total, the VALLEY dataset consists of 29 sampled pools from 29 wetlands. The WTL
154 dataset thus represents cladoceran community variation within wetlands, whereas the
155 VALLEY dataset represents community variation among wetlands at the valley scale.
156 When combined, the WTL & VALLEY dataset also represent variation among valleys at
157 the regional scale; there are 59 pools from 29 wetlands located in 4 valleys.

158

159

160 **Sampling**

161

162 We assessed a variety of pool characteristics during a sampling campaign in February-
163 March 2004, in the middle of the wet season. We determined the concentration of nitrates
164 (NO_3), total phosphate (TP), alkalinity, pH, conductivity, macrophyte coverage,
165 phytoplankton chlorophyll a, thickness of the sludge layer on the sediments, pool depth
166 and pool surface area. In addition, we assessed the density of potential predators
167 (cyclopoid copepods, mites, and larvae of the coleopteran genera *Ranthus*
168 (*Colymbetinae*) and *Hydroporus* (*Hydroporinae*). We refer to Coronel et al. (2004) for
169 methodological details on the collection of the data for these variables.

170 We collected cladoceran community data in two different ways: (1) by taking
171 snap shot samples of active communities at one sampling occasion, and (2) through the
172 analysis of dormant egg banks. These two methods have been shown to be
173 complementary in their ability to detect cladoceran species (Vandekerkhove et al. 2005a).
174 We sampled active communities during February-March 2004 by collecting water with a
175 tube sampler (75 mm diameter and 1.5 m length) from different places (vegetated and

176 non-vegetated areas) in the pool and by filtering this water through a 30- μm Nitex mesh.
177 The total filtered volume ranged between 3 and 15 L. Samples were preserved in sucrose-
178 formaldehyde solution (5% final concentration). We collected sediments with dormant
179 eggs at the beginning of the dry season of 2006 (26-29th of June). In each pool, we
180 collected sediment at ten haphazardly chosen locations using a KC-sediment core sampler
181 (0.7 meter long plexi-glass tube of 5.2 cm diameter). Only the upper three centimeters of
182 each core were retained (approximately 100 g wet weight per sample). A total amount of
183 one kilogram sediment per pool was collected. Immediately after collection, samples
184 were wrapped in aluminum foil and transported to the lab in a cooler box.

185

186

187 **Sample analysis**

188

189 We analyzed active community samples by counting a total of at least 300 individuals
190 from sub-samples. For the analysis of the sediment samples, we first isolated dormant
191 eggs by means of the Onbé-Marcus method as modified by Vandekerkhove et al. (2004).
192 After storage in the dark at 4 °C, we first removed gross material (mostly vegetal debris)
193 using sieves of 1 mm and 500 μm . Dormant eggs retained by a sieve of 63- μm mesh were
194 then isolated from fine debris by the sugar flotation method, following three steps: 1)
195 filtration through a 48- μm mesh, 2) centrifugation of the residual in a sugar solution
196 (1000 g table sugar in 1000 ml distilled water) at 3000 rpm for three minutes, and 3)
197 washing of the supernatant over a 48- μm size mesh using tap water. The isolated dormant
198 eggs (at least 300 eggs whenever possible) were next sorted according to morphology,

199 identified and counted under a stereo microscope (Olympus SZX12). To allow
200 identification to species level, we incubated unknown dormant egg types individually in
201 30-ml multi-well plates containing the Aachener Daphnien Medium (ADAM medium) at
202 a conductivity of $30 \mu\text{s cm}^{-1}$. Multi-well plates were placed in an incubator at 20°C with a
203 photoperiod of 14 hours light and 10 hours dark. Incubation medium was refreshed every
204 five days. For a period of two months, we checked all multi-well plates every four days
205 for emerging hatchlings. Hatchlings were transferred to 50-ml vessels and fed
206 *Scenedesmus obliquus* ($100.000 \text{ cells ml}^{-1}$) until a developmental stage at which they
207 could be identified. We used the keys of Pagui (1995) and Smirnov (1996) for
208 identification.

209

210

211 **Data analysis**

212

213 We compiled species lists for each of the pools, combining data from the active
214 community snapshot samples and the dormant propagule banks, and derived a presence-
215 absence dataset from these lists. We also calculated relative abundances of species using
216 the data from the snapshot samples of active communities.

217

218 *Geographic distance and environmental heterogeneity across spatial scales*

219 We calculated the mean geographic distance among pairs of pools for each of the three
220 levels of spatial scale, i.e. among pools within each individual wetland (WTL dataset),
221 among pools belonging to different wetlands within each valley (VALLEY dataset) and

222 among pools belonging to different valleys (WTL & VALLEY datasets combined). In the
223 same way, we used the environmental variables to estimate environmental heterogeneity
224 among pairs of pools at the within-wetland, the within-valley and the among-valley scales
225 as standardized Euclidean distances.

226

227 *Beta diversity of cladoceran communities across spatial scales*

228 We estimated beta diversity at each spatial scale following two different approaches: (1)
229 as the mean Bray-Curtis dissimilarity among pairs of pools, similar as for geographic
230 distance and environmental heterogeneity (i.e. among pools within wetlands using the
231 WTL dataset; among pools from different wetlands within valleys using the VALLEY
232 dataset, and among pools from different valleys). These calculations were done on the
233 presence-absence data derived from the species lists as well as on the relative abundance
234 data of the active communities; (2) through the application of diversity partitioning on
235 species richness of the species lists and true Shannon diversity (Jost 2007) estimated from
236 the abundance data of active communities. Species richness was partitioned in the
237 additive way, with $\gamma = \alpha + \beta_1 + \beta_2 + \beta_3$ (Lande 1996), where α refers to the average
238 richness in local communities (samples), gamma refers to the total richness observed in
239 the entire set of samples, and β_1 , β_2 and β_3 refer to the beta diversity at each of the
240 studied spatial scales: β_1 = among pools within wetlands; β_2 = among wetlands within
241 valleys; β_3 = among valleys. Additive diversity partitioning has the advantage that beta
242 components can directly be quantitatively compared with each other and with alpha and
243 gamma diversity. True Shannon diversity can only be partitioned in a multiplicative way,
244 but we transformed its alpha, beta and gamma components logarithmically (i.e., into

245 Shannon entropies) so as to make them relate additively (Jost 2007). A full hierarchical
246 partitioning analysis, including the three levels of spatial scale, could only be performed
247 on a subset of the WTL dataset, including all data of Taquina and Toro, but excluding the
248 data of Saito and San Ignacio. Incorporation of the latter valleys in the analysis would
249 have resulted in a bias, underestimating average beta diversity among wetlands (β_2),
250 because there were only data available for one wetland in each of these valleys. To assess
251 the robustness of these results and fully exploit the size of our dataset, we performed
252 additional partitioning analyses on our complete dataset, estimating beta diversity among
253 pools within each of the wetlands in the WTL dataset (β_1) as well as among pools
254 belonging to different wetlands in each of the valleys of the VALLEY dataset. Logically,
255 the latter variable incorporates both within- and among-wetland beta diversity within
256 valleys and should equal $\beta_1 + \beta_2$. Diversity partitioning calculations were performed with
257 the software PARTITIONv3 (Veech and Crist 2009).

258

259 *Explaining the beta components*

260 A commonly applied method to quantify the relative importance of alternative
261 metacommunity processes consists of the decomposition of community variation into an
262 environmental (E) and a spatial (S) component. Using direct gradient ordination
263 techniques (mostly redundancy analysis), statistical models are first constructed for both
264 components and their relative contributions to community variation are subsequently
265 assessed through variation partitioning (Borcard et al. 1992). Upon correction for the
266 spatial component, a significant environmental component (E/S) is generally accepted to
267 represent environmental control. A significant spatial component, after control for the

268 environmental component (S/E), can indicate neutral processes, historic events and
269 dispersal limitation (Legendre & Legendre 1998, Cottenie 2005), assuming that all
270 important environmental variables have been measured. The co-occurrence of significant
271 environmental and spatial components has been considered as being indicative of mass
272 effects (Cottenie 2005), although it can also represent species sorting that is partially
273 constrained by dispersal limitation (Ng et al. 2009).

274 To explain beta diversity in the cladoceran communities, we applied variation
275 partitioning on redundancy analysis models (RDA) for each of the three levels of spatial
276 scale, separately. For the largest spatial scale, i.e. the inter-valley scale, we constructed an
277 environmental and a spatial model using the entire dataset (VALLEY and WTL datasets
278 combined, $n = 59$). The environmental model (E) was constructed by applying the
279 forward selection procedure of Blanchet et al. (2008) to the environmental variables. For
280 the spatial model (V), we constructed a matrix representing valley identity using 3
281 dummy variables. With variation partitioning (Borcard et al. 1992, Legendre et al. 2005,
282 Peres-Neto et al. 2006), we then tested the marginal and unique contributions of the
283 environmental and spatial models in explaining community variation.

284 We applied the same procedures to the VALLEY dataset ($n = 29$) for the study of
285 beta diversity at the within-valley scale. However, the spatial model consisted here of two
286 components: (1) a V-component, representing valley identity using dummy variables (see
287 above), and (2) an S-component consisting of Moran's eigenvector maps (MEM) that
288 describe the spatial relationships among pools within individual valleys. MEM analysis
289 produces a set of orthogonal spatial variables, derived from the geographic coordinates of
290 the study sites (Dray et al. 2006). These variables represent spatial variation across a

291 range of spatial scales and can be used as explanatory variables in direct gradient analysis
292 to model spatial relationships in community data. In the S-matrix, the MEM variables
293 were arranged in blocks, each block corresponding to one valley. Within these blocks,
294 pools from the other valleys received the mean value 0. The structure of the blocks of
295 MEM variables in S were similar to that used to test the presence of different spatial
296 structures at different times, shown in Appendix C of Legendre et al. (2010). Appendix 1
297 provides an R function that can be used for the construction of a staggered matrix of
298 MEM spatial eigenvectors for sites that are spatially clustered. The type of MEM
299 variables computed in the present study were formerly called principal coordinates of
300 neighbour matrices (PCNM: Borcard and Legendre 2002, Borcard et al. 2004, Dray et al.
301 2006).

302 Using the VALLEY dataset, we then applied variation partitioning to assess the
303 unique contributions of the S- and E- model components to community variation, while
304 controlling for the V-component. An identical procedure was applied for studying
305 cladoceran variation at the intra-wetland scale using the WTL dataset ($n = 36$).

306 All analyses were carried out on the species lists (active and dormant community
307 data combined) as well as on the relative abundance data from the active communities.
308 We did the analyses on these two datasets because they should cast light on different
309 aspects of metacommunity dynamics. Indeed, we expect that analyses on abundance data
310 of active communities should mainly stress the impact of environmental gradients or
311 mass effects, because they emphasize shifts in the relative success of species and also
312 because these data were collected simultaneously with the environmental data. Analyses

313 on species lists should do better at reflecting distribution patterns of species; we expect
314 them to be more powerful in revealing patterns related to dispersal limitation.

315 All species data (both abundance and presence-absence) were Hellinger
316 transformed prior to analysis (Legendre and Gallagher 2001). After this transformation,
317 RDA and variation partitioning are based on the Hellinger distance, which is appropriate
318 for community composition data (presence-absence or abundance), instead of being based
319 on the inappropriate Euclidean distance; the Hellinger distance computed on presence-
320 absence data is monotonically related to the Ochiai distance, which is also appropriate for
321 community composition data. Of the environmental variables, conductivity, surface area,
322 sediment depth and chlorophyll *a* were log-transformed. Densities of predatory
323 invertebrate taxa tended to be positively correlated with each other; we summarized
324 overall predator density with the first principal component (i.e., sample scores vector) of
325 a standardized principal component analysis (eigenvalue: 39%). All statistical analyses
326 were performed in R (v2.8.1; R Development Core Team 2008), using the *rda* and *varpart*
327 functions of the *vegan* library (Oksanen et al. 2005, Peres-Neto et al. 2006), the
328 *forward.sel* function of the *packfor* library (Dray et al. 2007); MEM spatial
329 eigenfunctions were computed using the *PCNM* function of the *PCNM* library (Legendre
330 et al. 2009).

331

332

333 **Results**

334

335 **Geographic distance and environmental heterogeneity across spatial scales**

336

337 The mean geographic distance among pools increased by more than one order of
338 magnitude between successive levels of spatial scale (Figure 2A). The distance among
339 pools within wetlands (cf. WTL dataset) averaged 0.063 km. The mean distance among
340 pools of different wetlands within valleys (cf. VALLEY dataset) was 0.69 km, whereas
341 pools from different valleys were located at an average distance of 19.7 km from each
342 other (WTL and VALLEY datasets combined).

343 The mean Euclidean distances for environmental variables were highly variable, both
344 among individual wetlands as well as among valleys (Figure 2B). We detected no
345 tendency for higher heterogeneity at the valley scale compared to the wetland scale.
346 Heterogeneity among pools from different valleys also tended to be only slightly higher
347 than the within-wetland or within-valley means. See Appendix 2 for summary statistics of
348 the environmental variables.

349

350

351 **Patterns of beta diversity across spatial scales**

352

353 Although highly variable among wetlands and among valleys, mean Bray-Curtis
354 dissimilarities based on species lists tended to increase with spatial scale (Figure 2C). In
355 contrast, no such tendency was observed for Bray-Curtis dissimilarity based on the
356 relative abundance of species in active communities (Figure 2D).

357 A full hierarchical diversity partitioning analysis on the richness data of the
358 Taquina and Torro subset showed a substantial contribution of both the smallest ($\beta_1 =$

359 7.2) and largest spatial scales ($\beta_3 = 5.5$ species) to gamma diversity (Figure 3A, left
360 pane). Beta diversity among wetlands within valleys ($\beta_2 = 3.5$ species) was relatively
361 small. The additional partitioning analyses on the WTL and VALLEY datasets (Figure
362 3A, right pane) also showed a relatively high average beta diversity among pools within
363 wetlands (β_1) compared to the average beta diversity among pools from different
364 wetlands at the valley level ($\beta_1 + \beta_2$). According to a paired t-test, both estimates of beta
365 diversity could not be shown to differ significantly, indicating only a minor contribution
366 of β_2 to gamma diversity.

367 We observed similar patterns for Shannon diversity of active communities (Figure
368 3B). Full hierarchical diversity partitioning also indicated a small contribution of β_2 and a
369 relatively large contribution of β_1 and β_3 . Average beta diversity at the valley level
370 ($\beta_1 + \beta_2$; cf. VALLEY dataset) showed no significant difference with the average beta
371 diversity within wetlands (β_1 ; WTL dataset) according to a paired t-test ($p > 0.05$).

372

373

374 **Community variation and environmental gradients**

375

376 Appendix 3 gives a list of the species and their abundances in samples of active
377 communities and dormant propagule banks. Species lists differed significantly among
378 valleys (V- and V/E-components in Table 1A), with valley identity explaining up to 10.6
379 % of the community variation. pH proved to be the only significant environmental
380 variable (cf. E in Table 1A), although the effect of this variable was strongly reduced
381 upon correction for inter-valley differences (E/V in Table 1A left). Within valleys and

382 wetlands, MEM models showed no evidence for spatial patterns. Environmental models
383 explained significant fractions of the variation in the species lists of the WTL and
384 VALLEY datasets, but these effects became non-significant when the identity and MEM
385 models of valleys and wetlands were taken into account, respectively (Table 1B and C
386 left).

387 At the inter-valley scale, the composition (in terms of relative abundance) of the
388 active cladoceran communities was significantly explained by both the environmental
389 model (consisting of the variables alkalinity, sludge depth and surface area) and by valley
390 identity, although the environmental model explained approximately 3 times more
391 variation than valley identity (See E-, V-, E/V- and V/E-components in Table 1A right).
392 Analyses at the within-valley level using the VALLEY dataset (Table 1B right) revealed
393 no significant spatial patterns, whereas the explanatory power of the environmental
394 model was low (only marginal effects were significant). At the within-wetland level
395 (WTL dataset, Table 1C right), the marginal and conditional effects of the environmental
396 model (based on alkalinity, surface area, sludge depth and the predation gradient)
397 amounted to 21% and 17% of explained variation, respectively. At this level of spatial
398 scale, the MEM model explained no community variation.

399

400

401 **Discussion**

402

403 In our study, geographic distances among pools increased with more than one order of
404 magnitude across each level of spatial scale. This, however, translated only in a weak

405 increase in environmental heterogeneity and some individual wetlands encompassed a
406 degree of pool heterogeneity similar to what was present at the landscape scale. We found
407 this high within-wetland heterogeneity to concur with relatively high cladoceran beta
408 diversity, both in terms of species richness and Shannon diversity. With RDA analysis,
409 we were able to uniquely explain part of the variation among active communities by
410 environmental gradients, which suggest that this beta diversity at the wetland scale is
411 structured by environmental heterogeneity (Cottenie and De Meester 2004). Part of the
412 unexplained beta diversity may also have originated historically by chance (cf. priority
413 effects; Louette and De Meester 2007, Loeuille and Leibold 2008), although we have no
414 specific data to further support this idea. We found no evidence for spatial community
415 patterns within wetlands.

416 Beta diversity at the valley scale was not higher than at the scale of individual
417 wetlands, despite the larger average distance among pools. Within valleys, environmental
418 heterogeneity could not be shown to be consistently higher than within wetlands and
419 RDA-models were not able to significantly explain beta diversity. This suggests that
420 environmental control was probably not more important as a generator of beta diversity at
421 this spatial scale than at the within-wetland scale. Absence of spatial patterns also
422 suggests no important dispersal limitation within valleys.

423 In contrast, beta diversity among valleys tended to be relatively high. RDA-
424 analyses demonstrated strong differences among valleys, especially for species lists. Such
425 pattern may be generated by neutral dynamics and dispersal limitation but could also
426 indicate control of community composition by large-scale environmental gradients.
427 RDA-analysis on species lists indeed suggested an association between species

428 distribution patterns with a pH-gradient, but variation partitioning revealed that the
429 importance of large scale pH variation could not be unequivocally evaluated, whereas
430 among-valley community differentiation proved robust. Reduced exchange of propagules
431 among pools at this scale is indeed very plausible given the morphology of the landscape
432 (mountain ridges, lack of hydrological connections) and the distance among valleys
433 (ranging between 4 and 28 km). Large mammals can be important vectors for the
434 dispersal of cladoceran dormant eggs (Vanschoenwinkel et al. 2008) and in our study
435 area llamas (*Lama glama*) are good candidates for such zoochorous dispersal. Llamas are
436 mainly herded in the vicinity of farms, and these animals may therefore be responsible for
437 much of the exchange of dormant eggs between pools within wetlands and among
438 wetlands within valleys but they may be less important as dispersal vectors among
439 valleys.

440 The RDA-analyses on the relative abundance data of active communities also
441 indicated a tendency towards differentiation among valleys, but this pattern was
442 considerably weaker than with species lists. One can indeed expect that analyses on
443 abundance data will be less efficient in revealing patterns of species distributions because
444 they tend to be confounded mainly by abundance patterns of dominant and subdominant
445 species. However, analyses on abundance data may be more sensitive to responses of
446 communities to environmental gradients because they emphasize shifts in the relative
447 success of species that perform differently along these gradients. In our study, the
448 abundance data were explained by similar sets of environmental variables at the largest
449 and smallest of spatial scales (e.g., alkalinity, surface area and sludge depth). The effect
450 of these variables at the largest spatial scale seemed, however, mainly a reflection of their

451 effect at the smallest scale. Indeed, the gradient lengths of these variables were only
452 slightly larger at the inter-valley scale than at the wetland scale, and variation partitioning
453 based on the entire dataset showed that the explanatory power of the environmental
454 model (E) was only slightly reduced when among-valley differences were controlled for
455 (E/V; see Table 1). This indicates that large scale environmental heterogeneity was of
456 minor importance in explaining cladoceran community variation.

457 Several field studies have attempted to assess the relative importance of
458 environmental control, mass effects, neutral processes and dispersal limitation for
459 zooplankton metacommunities. These studies were performed on a variety of water body
460 types with different connectivity levels at a wide range of spatial scales. From these
461 studies, environmental control seems to come out most frequently as the dominant
462 metacommunity organizing principle. In a system of neighboring, strongly interconnected
463 ponds, Cottenie et al. (2003) found that environmental control generated an important
464 degree of differentiation among communities despite the homogenizing effect of water
465 exchange via rivulets. In a set of temporary rock pools on a small scale rock shelf,
466 Vanschoenwinkel et al. (2007) also concluded environmental control to be the most
467 important metacommunity structuring process, together with some indications for mass
468 effects among interconnected pools. Pandit et al. (2009) showed the degree of
469 environmental control to depend on the degree of habitat specialization. At a much larger
470 spatial scale, Beisner et al. (2006) mainly found evidence for environmental control in a
471 set of connected lakes. Although abundance data showed spatial patterns, these patterns
472 were not reflected in the presence- absence dataset, as abundant zooplankton species were
473 not restricted in their spatial distribution. Based on a meta-analysis of a large number of

474 datasets of a variety of organism groups along a broad gradient of spatial scales, Cottenie
475 (2005) concluded that passive dispersers overall tend to track well environmental
476 heterogeneity, although the importance of dispersal limitation appears to increase at the
477 expense of environmental control at the larger spatial scales, probably because species
478 fail to reach habitat patches that match with their niche requirements.

479

480

481 **Conclusions**

482

483 To our knowledge, our study is the first to simultaneously study metacommunity
484 structure of a passively dispersing animal group at three levels of spatial scale along a
485 range of inter-patch distances of at least two orders of magnitude. The detailed analysis of
486 resting egg banks also allowed us to complement data obtained from active community
487 samples to establish a high quality presence-absence dataset, yielding reliable species
488 distribution patterns that are otherwise difficult to obtain from active community
489 sampling alone (Vandekerkhove et al. 2005a). Our study presents a case where
490 environmental control seems to be the dominant metacommunity structuring process at
491 the smallest spatial scale. However, an increase in spatial scale coincided with a marked
492 increase in beta diversity that appears to be mainly generated by dispersal limitation. Our
493 study is well in line with the results of Cottenie (2005) but illustrates that larger spatial
494 scales need not necessarily be associated with stronger environmental gradients, which in
495 some cases may also explain the lack of evidence for stronger environmental control at
496 these scales. Extrapolation of spatial diversity patterns in cladoceran metacommunities to

497 other organism groups should be done with caution. However, we believe that our results
498 may represent general patterns that also hold for other aquatic organisms with similar life
499 history and dispersal strategies (e.g., short generation times, production of dormant
500 stages, passive dispersal). Candidate organism groups are large branchiopods and small
501 invertebrate taxa like rotifers, ostracods, turbellarians, and nematodes.

502

503

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614 Table 1. Partition of variation in cladoceran communities at three levels of spatial scale using partial RDA analysis on relative
615 abundance data of active communities and species lists (active communities and dormant propagule banks combined). E:
616 environmental model; S: spatial model component, constructed from MEM variables; V: model component representing the 4
617 individual valleys; WTL: model representing the 6 individual wetlands; E/(S+V): environmental model corrected for valley identity and
618 spatial patterns within valleys; E/(S+WTL): environmental model corrected for wetland identity and spatial patterns within wetlands.
619 R^2_{adj} (%): community variation explained by model, expressed in %; df_{model} : degrees of freedom of model; df_{res} : residual degrees of freedom.
620

	Species lists					Abundance data of active communities				
	R^2_{adj} (%)	df_{model}	df_{res}	F	P	R^2_{adj} (%)	df_{model}	df_{res}	F	P
A) Inter-valley scale										
WTL & VALLEY dataset, $n = 59$										
E	4.1 ^a	1	57	3.49	0.001	9.9 ^d	3	55	3.12	0.001
V	10.6	3	55	3.19	0.005	4.1	3	55	1.82	0.020
E/V	0.5	1	54	1.28	0.191	9	3	52	2.91	0.001
V/E	6.5	3	54	2.38	0.001	3.3	3	52	1.69	0.027
B) Within-valley scale										
VALLEY dataset, $n = 29$										

E	11.9 ^b	3	25	2.26	0.001	4.9 ^e	1	27	2.43	0.031
S	1.3	8	20	1.05	0.389	11.9	8	20	1.47	0.072
V	8.2	3	25	1.83	0.010	2.9	3	25	1.28	0.220
E/(S+V)	-0.5	3	14	0.97	0.526	-0.6	1	16	0.88	0.456
S/(E+V)	1.3	8	14	1.04	0.433	12.6	8	16	1.46	0.112

C) Within-wetland scale

PLT dataset, *n* = 35

E	8.5 ^c	1	33	4.15	0.001	20.8 ^f	4	30	3.23	0.001
S	-5.6	10	24	0.82	0.907	2.4	10	24	1.08	0.339
WTL	14.5	5	29	2.15	0.001	8.7	5	29	1.65	0.024
E/(S+WTL)	1.6	1	18	1.36	0.196	17.4	4	15	2.25	0.001
S/(E+WTL)	2.0	10	18	1.07	0.337	2.0	10	15	1.08	0.362

621 a: environmental model constructed from the environmental variable pH

622 b: environmental model constructed from the environmental variables chlorophyll a, depth and total phosphorus

623 c: environmental model constructed from the environmental variable pH

624 d: environmental model constructed from the environmental variables alkalinity, sludge depth and surface area

625 e: environmental model constructed from the environmental variable TN

626 f: environmental model constructed from the environmental variables alkalinity, sludge dept

627 **Legend to Figures**

628

629 Figure 1. Location of the four valleys sampled in the Tunari mountain range
630 (Cochabamba, Bolivia) and a schematic representation of the wetlands (represented by
631 ovals) and pools (represented by circles) sampled in each valley. Filled symbols represent
632 pools sampled for the VALLEY-dataset. Empty circles represent pools that were
633 additionally sampled for the WTL-dataset.

634

635 Figure 2. Average geographic distance (A), environmental heterogeneity (B) and
636 community dissimilarity (C,D) among pools across the three levels of spatial scale (i.e.,
637 within wetlands, among pools of different wetlands within valleys and among pools of
638 different valleys). Environmental heterogeneity was calculated as the standardized
639 Euclidean distance for the environmental variables. Community dissimilarities were
640 calculated as the Bray-Curtis distance among pools based on species lists (presence-
641 absence data derived from the combined data of active communities and dormant
642 propagule banks, C) as well as on the relative abundance data of the active communities
643 (D). Stars represent individual wetlands and valleys; circular symbols represent averages
644 and error bars denote the standard deviation.

645

646 Figure 3. Diversity partitioning results for species richness (A) and Shannon entropy (B).
647 The left panels in the graphs represent the results of a full hierarchical analysis on the
648 Taquina and Toro subset. The right panels represent average results for each wetland and
649 each valley in the WTL- and Valley-datasets, respectively. Alpha: local pool diversity;

650 Beta1: beta diversity among pools within wetlands; Beta2: beta diversity among wetlands
651 within valleys; Beta3: beta diversity among valleys. Beta diversity among pools in the
652 VALLEY-dataset comprises both Beta1 and Beta2 and is therefore denoted as
653 Beta1+Beta2. Error bars represent the standard deviation.
654

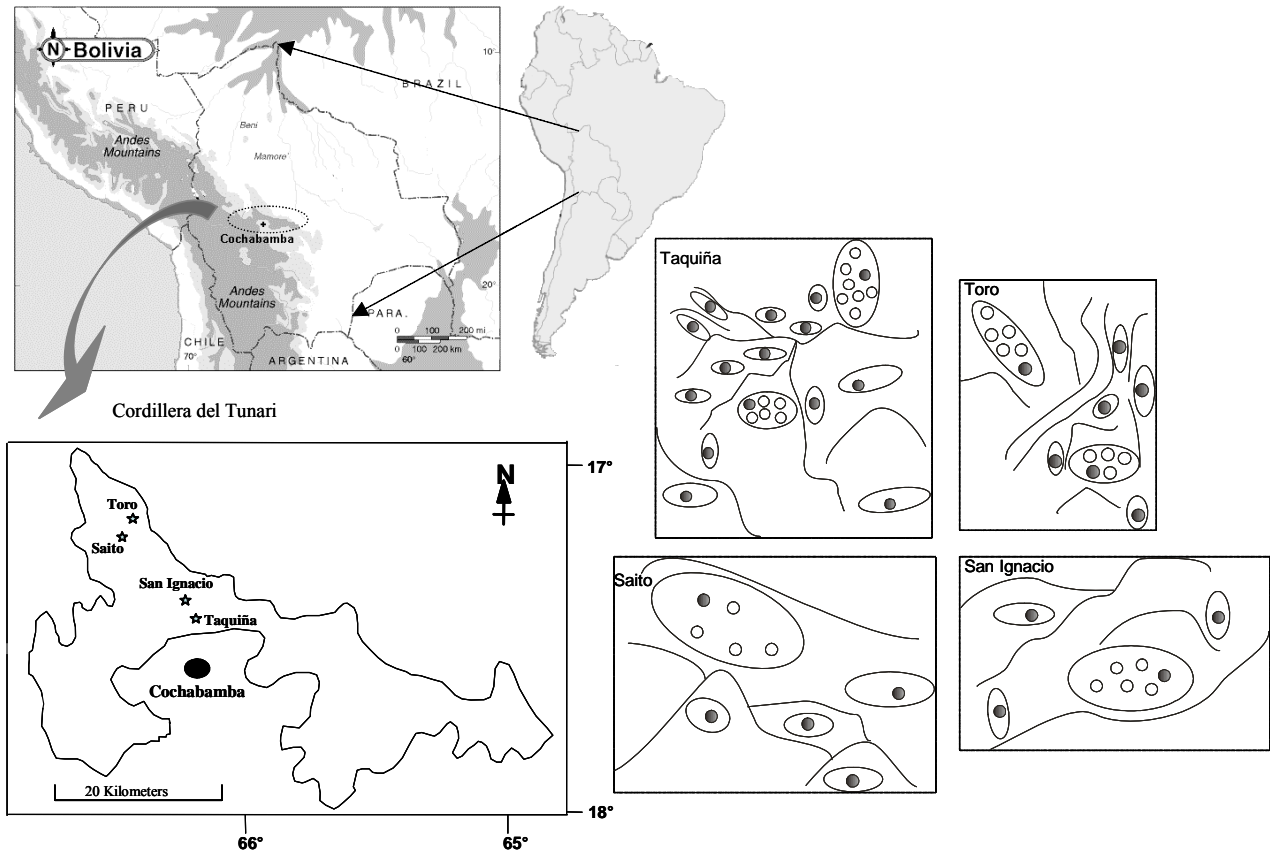
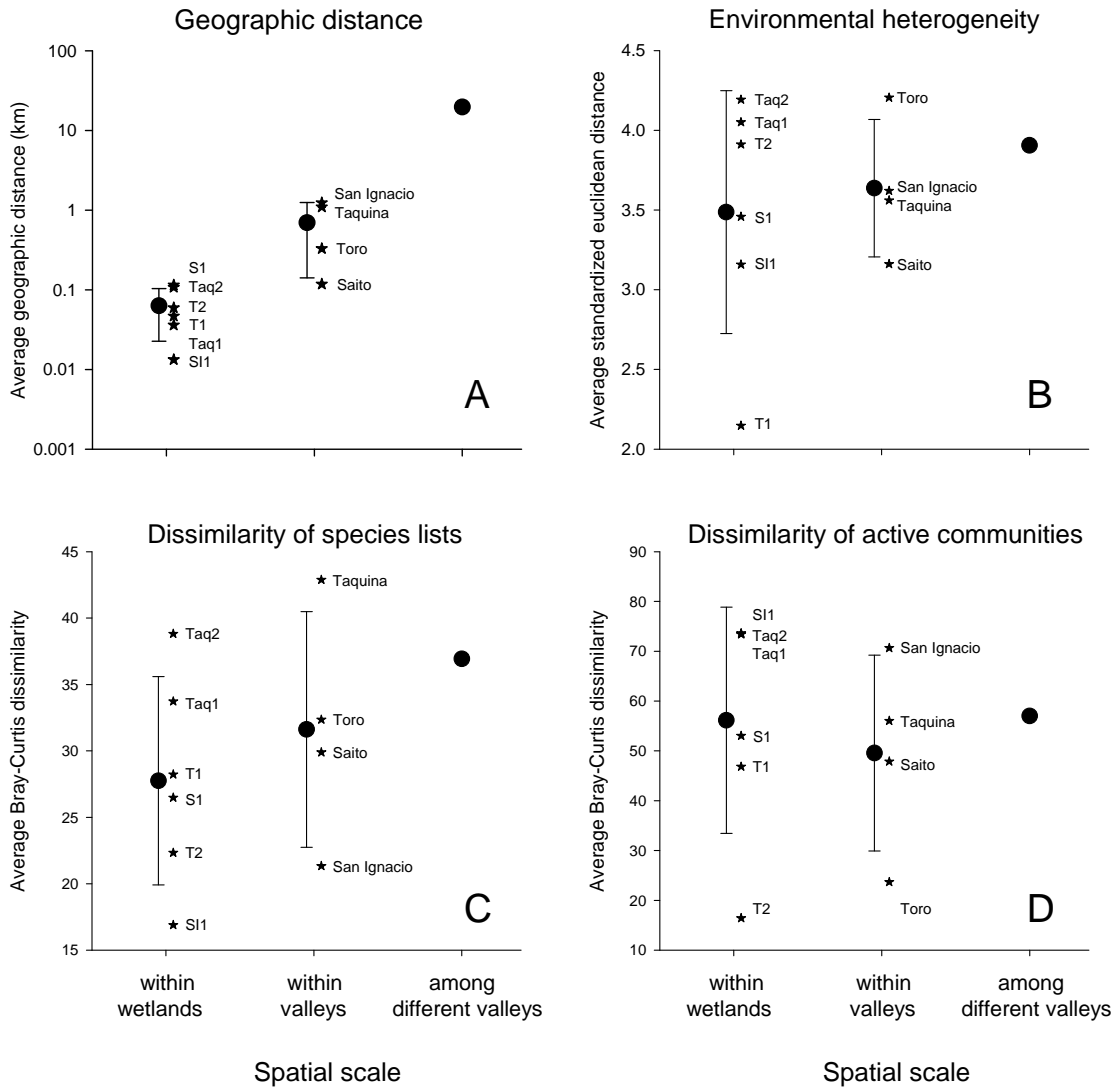
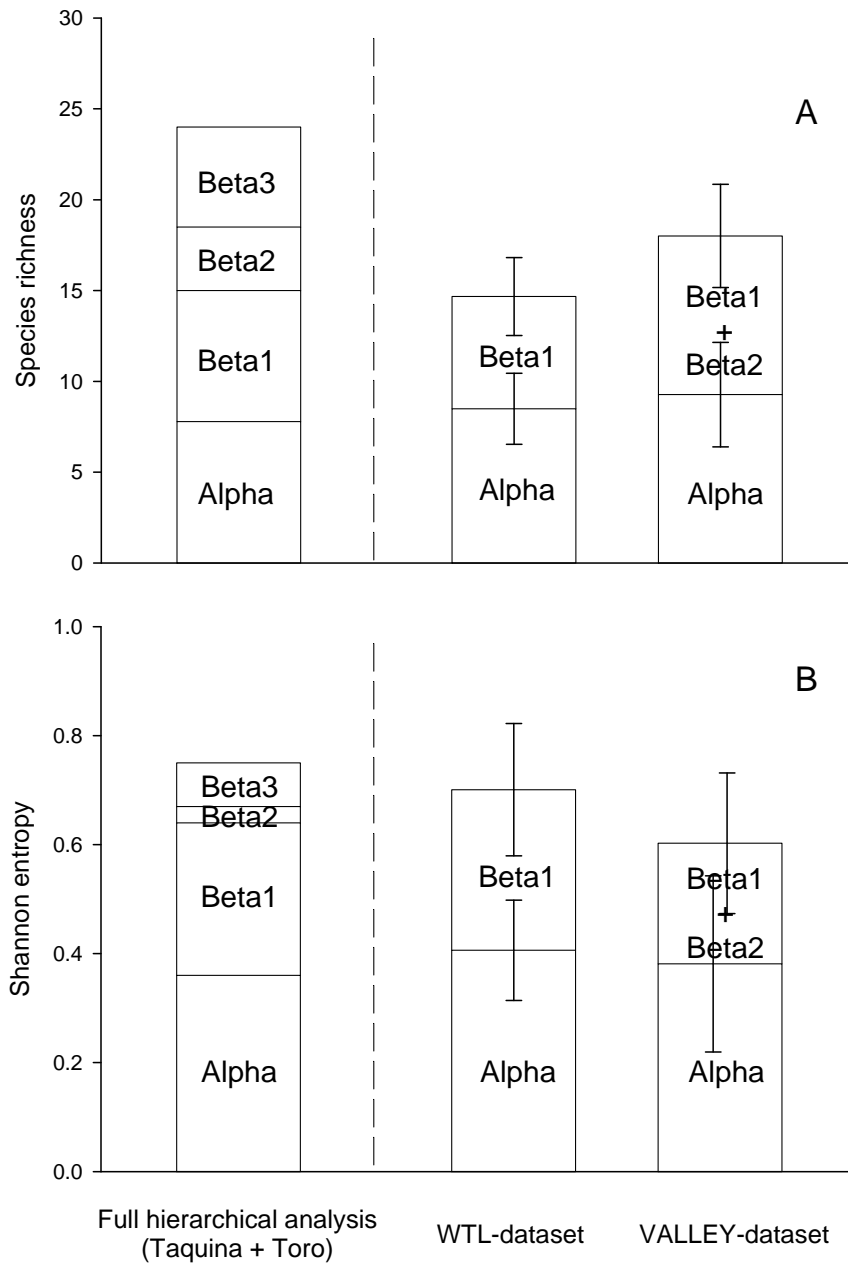


Figure 2, Steven Declerck et al.



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Figure 3, Steven Declerck et al.



Appendix 2: Environmental variables with their medians, quartiles, minimum and maximum values. med: median; 25%: 25 percentile, 75%: 75 percentile; max: maximum recorded for the entire dataset.

	med	min	max	25%	75%
Chlorophyll a ($\mu\text{g/l}$)	11	2	154	5	18
Macrophyte cover (%)	70	0	100	50	90
pH	7	5	10	7	8
Conductivity ($\mu\text{S/cm-1}$)	15	5	238	12	19
Alkalinity (mg/l CaCo_3)	9	0	31	6	13
Oxygen (mg/l)	6	3	12	5	7
Total nitrates (mg/l)	0.08	0.01	0.36	0.05	0.13
Total phosphates (mg/l)	0.01	0.00	0.63	0.01	0.01
Transparency (m)	0.35	0.11	0.50	0.29	0.39
Depth (m)	0.19	0.03	0.46	0.13	0.27
Surface area (m ²)	23	2	310	8	52
Sludge depth (m)	0.25	0.02	0.60	0.10	0.40
Altitude (m)	4327	4067	4429	4252	4383

Appendix 3: Occurrence and abundance of cladoceran species, as determined from the analysis of the dormant propagule banks and snap shot samples of the active communities. Occ: number of pools with the species; %occ: frequency of occurrence; med: median; 25%: 25 percentile, 75%: 75 percentile; max: maximum recorded for the entire dataset.

	Dormant propagule bank samples						Active community snap shot samples					
	occ	%occ	med ^a	25% ^a	75% ^a	max ^a	occ	% occ	med ^b	25% ^b	75% ^b	max ^b
<i>Alona boliviana</i>	3	5	0	0	0	35	1	2	0	0	0	62
<i>Alona cambouei</i>	42	69	13	0	36	159	39	64	1	0	3	28
<i>Alona davidi</i>	17	28	0	0	5	128	11	18	0	0	0	14
<i>Alona glabra</i>	4	7	0	0	0	22	0	0	0	0	0	0
<i>Alona ossiani</i>	55	90	34	12	72	247	47	77	2	0	9	59
<i>Alonalla excisa</i>	30	49	1	0	12	72	40	66	1	0	3	58
<i>Bosmina huaronensis</i>	0	0	0	0	0	0	1	2	0	0	0	0
<i>Camptocercus aloniceps</i>	23	38	0	0	12	60	18	30	0	0	0	44
<i>Ceriodaphnia</i> sp.	29	48	1	0	17	94	15	25	0	0	0	63
<i>Chydorus brevilabris</i>	52	85	22	11	41	119	56	92	18	4	88	500

<i>Daphnia peruviana</i>	5	8	0	0	0	4	4	7	0	0	0	2
<i>Daphnia pulex</i>	7	11	0	0	0	46	5	8	0	0	0	6
<i>Ephemerophorus hibridus</i>	7	11	0	0	0	162	2	3	0	0	0	18
<i>Ephemeroporus cf. acanthodes</i>	0	0	0	0	0	0	1	2	0	0	0	1
<i>Graptoleberis testudinaria</i>	11	18	0	0	0	41	8	13	0	0	0	10
<i>Drepanothrix cf. dentata</i>	2	3	0	0	0	17	0	0	0	0	0	0
<i>Macrothrix atahualpa</i>	53	87	55	20	102	232	45	74	1	0	14	97
<i>Paralona piagra</i>	6	10	0	0	0	17	3	5	0	0	0	91
<i>Pleuroxus caca</i>	0	0	0	0	0	0	7	11	0	0	0	7
<i>Pleuroxus cf. aduncus</i>	2	3	0	0	0	7	0	0	0	0	0	0
<i>Pleuroxus sp1</i>	6	10	0	0	0	32	0	0	0	0	0	0
<i>Schapholeberis spinifera</i>	1	2	0	0	0	4	1	2	0	0	0	1
<i>Simocephalus mixtus</i>	47	77	18	1	50	198	32	52	0	0	3	142
<i>Streblocerus serricaudatus</i>	5	8	0	0	0	55	0	0	0	0	0	0
<i>Ilyocryptus cf. spinifer</i>	1	2	0	0	0	7	0	0	0	0	0	0

^a number of dormant propagules per kilogram of sediment wet weight

^b numbers of individuals per liter