Chapter 5
Diversity of Aquatic Macroinvertebrates Along Altitudinal Gradients in Colombia

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5.1 Introduction

Mountains hold fundamental challenges to aquatic macroinvertebrates. As ectotherms, macroinvertebrates are being challenged to adapt or track changes in their environment, either in time through a behavioral shift or in space by an altitudinal shift. Recent evidence shows that such a dynamic, to adapt or to track, is mainly driven by the water temperature and oxygen availability, as well as the metabolic thermal sensitivity of each species (Jacobsen 2020). As such, by considering the interactions of these three modulators, it will be feasible to model diversity patterns along altitudinal gradients across the globe. However, such a generalization is not straightforward, for temperate and tropical macroinvertebrates may exhibit similarly narrow thermal breadths at higher latitudes but contrasting thermal breadths at lower elevations (Shah et al. 2017).

The narrowest thermal breaths in tropical low elevations open a new research agenda on the drivers of community organization in Tropical rivers. In these rivers, other factors are expected to drive the assembly of aquatic communities as species thermal tolerances are not necessarily linked to the variability in water temperature and oxygen (Shah et al. 2017; Jacobsen 2020). For example, in the Colombian Mountain chains, where the variability of environmental factors responds to some degree to the altitudinal shifts (González-Trujillo et al. 2021), it is expected that

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invertebrate diversity responded linearly to the elevation-driven environmental variability. However, mounting evidence is demonstrating that neither the species richness nor species occurrence is linearly correlated to elevation. Recent studies have demonstrated that such nonlinear responses may be partially explained by other factors, such as biogeographical legacies or urbanization intensity.

In this chapter, we review studies assessing the altitudinal distribution shifts of macroinvertebrates communities across tropical Andean streams. We focus on assessing the distribution of the species from different macroinvertebrate orders across the Colombian mountains and how it relates to the elevational-driven changes in the environmental conditions of the streams. Chapter 1 describes how the altitudinal gradient is a modulator of climatic variables (e.g., temperature, precipitation, and relative humidity). Environmental factors of tropical streams present a wide variation across latitudinal (Morales-Castilla and García-Valdés 2014) and altitudinal gradients (Rahbek 2005). These factors are considered as major "engines" that perform structural and functional attributes into aquatic ecosystems (Vannote et al. 1980). Therefore, we explore relations between climatic variables and their relations with structural (e.g., density, biomass, abundance, richness, etc.) and functionals (e.g., energy fluxes) aspects in the communities and ecosystems. We also introduce to alternative explanations to the species turnover among altitudinal ranges which have been proposed in past years.

5.2 Altitudinal Changes in Diversity of Different Taxonomic Groups

A long-standing civil conflict has partially truncated the study of Colombian diversity. Due to social conflict that has affected to Colombia for more than 60 years, the western and the south of the country have been few explored (Sabater et al. 2017), being the Andean and Caribbean regions where more studies have been conducted so far. In this sense, the patterns presented in this section are unavoidable geographically biased. Yet, they provide evidence of non-linear relationships between elevation and macro invertebrate richness.

In the Colombian mountain systems, such as the Sierra Nevada de Santa Marta-SNSM (north of Colombia), we observed two general patterns of altitudinal shifts: (1) the decreasing richness with increasing altitude, and (2) the increase of richness at intermediate altitudes (McCoy 1990; Brehm and Fiedler 2003). The first statement supports the Rappaport rule (Stevens 1992), while the second one supports the idea that "extremes are bad." In the second statement, environmental extremes are thought to occur in altitudinal extremes and then, diversity peaks at intermediate elevations, where environmental conditions are more suitable for organisms' persistence (Jacobsen 2020). Whether one of the two patterns is found depends on the taxonomic group being studied, as responses to elevation-driven constraints of *Leptohyphes* mayflies are different from that of Chironomidae dipterans.

In this section, we provide a brief review of the distributional patterns observed across different taxonomical orders of macroinvertebrates.

Ephemeroptera This order is one of the most widely studied groups in Colombia in two last decades (Roldán et al. 2014). The first works that included elevational gradients were made by Roldán (1980, 1985) in the Antioquia department at Andean Mountain. For rivers of the Tolima Department (Central Mountain Range of the Colombian Andes), genera *Baetodes*, *Camelobaetidius*, *Leptohyphes*, and *Thraulodes* occupy the entire altitudinal range (340–1555 masl) (Vásquez-Ramos and Reinoso 2012). *Leptohyphes* (Ephemeroptera: Leptohyphidae) is a genus well studied in Colombia, especially at the species level (Molineri et al. 2002, 2011; Molineri and Zúñiga 2004, 2006). For this reason, we analyzed the altitudinal distribution of *Leptohyphes* in the SNSM as a model taxon, using presence-absence data of species from 2000 to 2017. The altitudinal tendency of leptohyphids species showed a lower richness in the lower and headstream sections of the gradient, and higher diversity in the middle section (Fig. 5.1a). The unique species reported in the low zone was *L. jodiannae* (60 masl). *L. coconuco* (1700 masl) was present in the high sector, and in the middle section, eight species were found (including the two species mentioned above).

Odonata Tobias-Loaiza and Tamaris-Turizo (2019) reviewed the spatial and temporal distribution of Odonata order in eight rivers of three flanks in the SNSM, finding a wide altitudinal distribution of this order, especially of the genera *Erythrodiplax, Sympetrum* (both of Libellubidae family: 50–2800 masl), and *Hetarerina* (Calopterygidae: 50–1800 masl), being *Archilestes* (Lestidae) genus with lower

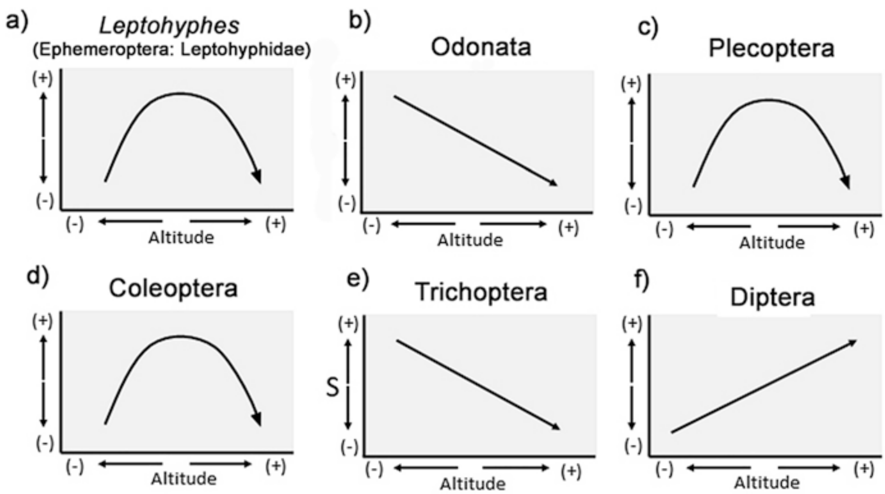

Fig. 5.1 Distribution models of the diversity of some select groups of aquatic insects along of the altitudinal gradient (**a**) *Leptohyphes* (Ephemeroptera: Leptohyphidae), (**b**) Odonata, (**c**) Plecoptera, (**d**) Coleoptera (**e**) Trichoptera (**f**) Diptera

distribution from 600 to 900 masl. The highest richness was found in the lower and middle sections of the basins. *Triacanthagyna*, *Telebasis*, *Micrathyria*, *Miathyria*, *Gynacantha*, *Enallagma*, *Caryphaeshna*, *Archaeogomphus*, and *Agriogomphus* were only reported in the lower zone. As such, evidence suggest that the diversity of Odonata decreases as the altitudinal gradient increases (Fig. 5.1b). This type of distribution, which is commonly observed in this order, is attributed by some authors to the intermediate disturbance hypothesis (Connell 1978), which states that diversity is low after a disturbance when few species have survived, and is high when a disturbance occurs with intermediate frequency or intensity. Human impacts favor the development of favorable environments, such as artificial and temporary ponds and phytotelmata systems, which promote the establishment of Odonata. Similar results were found by Cuellar-Cardozo et al. (2020) in the Paicol River (southwest of Colombia, in the Huila Department), which registered the highest abundances and richness in a heterogeneous area, with the presence of cattle, and near to urban zone and relicts of native forest.

Plecoptera The stoneflies present a variable richness along the altitudinal gradient. In the SNSM, the stoneflies show the higher richness in the middle section of their altitudinal distribution (from 500 to 1800 masl) (Fig. 5.1c). This group of organisms has been little studied, but it is known that *Anacroneuria* is the genus-dominant in Colombia (Rúa-García et al. 2015). In the abundance and distribution of stoneflies, the focus in the altitudinal gradient might be made at the species level. In the Andean zone, their richness has been evaluated from 60 to 2000 masl, with the high zone as the one with the highest richness. In the SNSM, is interesting that endemic species are principally located in the middle and the higher zones, over 1200 masl (e.g., *A. tayrona*, located above 1700 masl) (Tamaris-Turizo et al. 2007). Other species, as *A. caraca* and *A. marta,* have shown a lower altitudinal distribution (20–100 masl) (Unpublished data).

Coleoptera For coleopterans, the altitudinal distributions of the genera are not clear, although they could parallel Plecoptera distributional patterns (Fig. 5.1d). González-Córdoba et al. (2015) carried out a study about the distribution of species of Coleoptera in the Valle del Cauca Department (located in the south-west of Colombia); the organisms corresponded to samples taken from 1991 to 2014, in 63 fluvial systems across an altitudinal range from 0 to 2600 masl of 14 genera; only *Stenhelmoides*, *Xenelmis*, and *Onychelmis* showed a restricted distribution (at 400, 1400, and 1800 masl respectively). These observations could be associated with the wide environmental range of these taxa (González-Córdoba et al. 2020). Despite these studies, it is necessary to develop more work on the altitudinal distribution of coleopterans in Colombia.

Trichoptera A study carried on caddisflies (Trichoptera) of the Gaira River (SNSM) showed that *Amazonatolica*, *Cyrnellus*, *Nectopshyche*, and *Polycentropus* preferred the high part of the basin, in the middle sector the more representative taxa were *Ochotrichia*, *Cerasmatrichia,* and *Metrichia* (reach with the lowest abundance), while in the low basin the organisms more dominant were *Protoptila*, *Mortoniella*, *Oecetis*, and *Chimarra* (Oliveros-Villanueva et al. 2020). Previously, Serna-Macías et al. (2015) studied the distribution of caddisflies in the lower section (60–360 masl) of the Manzanares River (SNSM) and found 14 genera in the higher section, and eight genera in the lower sector. In addition, the abundance decreased with the reduction of the altitudinal gradient (from 1353 to 148 individuals) (Fig. 5.1e). Contrary to these results, González-Vargas and García-García (2021) evaluated the altitudinal distribution of Trichoptera in the Palmar River, located in the Cundinamarca Department (East Andean Mountain), in an altitudinal range from 1090 to 3294, and found a high richness in the headstream and a decrease in diversity according to decline in the altitudinal gradient; *Neotrichia* (Hydroptilidae), *Triplectides* and *Oecetis* (Leptoceridae), and *Contulma* (Anomalopsychidae) were genera with distribution restricted to headwaters. In the Tolima Department, genus *Smicridea* is distributed along the altitudinal gradient (340–1555 masl), but *Culoptila*, *Helicopsyche*, and *Atopsyche* prefer high areas, whereas *Protoptila*, *Neotrichia*, and *Chimarra* are located at low elevation (Vásquez-Ramos and Reinoso 2012).

Diptera Unpublished data of SNSM show some tendencies in genera of Chironomidae (Diptera) related to the altitudinal gradient. The most diverse reaches were located in the middle zones (12 genera), followed by high- (11 genera), and low-altitude zones of the basin (8 genera). In addition, at the subfamily level, Orthocladiinae exhibited the highest abundances and number of species in the high reaches, whereas Tanypodinae in the middle, and Chironominae in the lower sectors of the basin, respectively. However, when considering only individual abundance, low and middle sectors showed higher similarity compared with high-altitude sectors (Fig. 5.1f). Yet, such a pattern may change depending on the location along the Andean chain. In a parallel study performed in the Tolima Department, for instance, Vásquez-Ramos and Reinoso (2012) found that Chironominae, Orthocladiinae, and Tanypodinae did not show preferences for certain altitudinal zones and were recorded in all the stations of the elevation gradient (340–1555 masl).

In Andean streams of the city of Bogotá and other surrounding areas, with an altitudinal range between 2500 and 3200 masl, Buitrago-Guacaneme et al. (2018), Cuadrado et al. (2019), and Rodríguez-Rodríguez et al. (2021) studied the distribution gradients of the aquatic Diptera, especially regarding the black flies of the Simuliidae family. The first of these studies showed that some black fly species, such as *Simulium muiscorum*, had a pattern contrary to dissolved oxygen, temperature, and current velocity so that their distribution seems to increase at the sites with lower elevation and a relatively higher degree of contamination. On the contrary, the species *S. ignescens* was associated with slightly more oxygenated waters of the upper sectors of four streams analyzed (Buitrago-Guacaneme et al. 2018). Complementarily, Cuadrado et al. (2019) found that *S. muiscorum* had a widespread niche and that it can be in high localities, but whose water quality conditions are moderate; for these authors, *S. ignescens* was also common in the middle parts of the streams with medium pollution conditions, while another species (e.g., *Gigantodax ortizi*) were dominant in the high and intermediate sectors of the rivers.

From these investigations, it can be deduced that the different black-flies species prefer some sectors of the altitudinal gradients, but this response interacts with the water quality.

For other groups of Diptera, the study by Rodríguez-Rodríguez et al. (2021) showed that the families Psychodidae, Limoniidae, Pericelididae, and Blephariceridae, and chironomid subfamilies such as Podonominae (which is characteristic of high mountain river systems, Acosta and Prat 2018) and Chironominae are restricted to the upper basin of the Fucha River. Meanwhile, families such as Muscidae, Simuliidae, Dolichopodidae, Ceratopogonidae, and Empididae, and the Orthocladiinae (subfamily of Chironomidae) preferred the middle and lower part of the Bogotá and Fucha river basins. In these fluvial systems, the most polluted are in the lower basin, close to urban influence, which seems to promote the dominance of some genera of the Chironomidae, especially *Corynoneura* and *Cardiocladius*, while genera such as *Larsia*, *Parochlus*, *Podonomus*, *Thienemanniella*, *Riethia*, and *Tanytarsus* have a greater representation in the upper sectors of the rivers (Fig. 5.2). It is important to highlight that these authors found that neither pH nor dissolved oxygen showed a clear association with the presence of Diptera genera along the altitudinal gradients.

Recently, Villamarín et al. (2021) studied the diversity and altitudinal distribution of chironomids in the Ecuadorian Andes. The study was carried out at El Oro Province (Southwestern Ecuador) and the samples were taken in an altitudinal range from 10 to 2427 masl. The results showed that the high-altitude zones had low

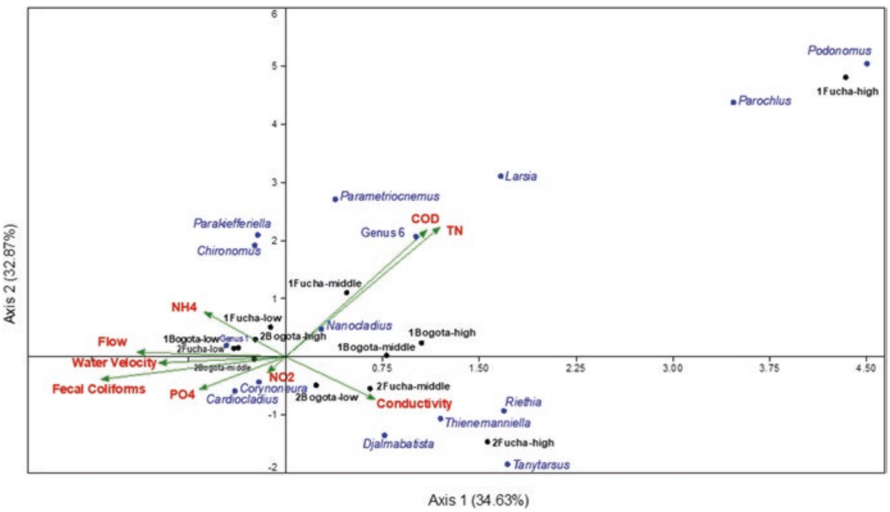

Fig. 5.2 Canonical correspondence analysis of the Chironomidae family genera in the Fucha and Bogotá rivers, Colombian Andes. Number 1 corresponds to the rainy season and number 2 to the dry period; COD chemical oxygen demand, TN total nitrogen, NH_4 ammonium, NO_2 nitrite, PO_4 orthophosphate. (Modified from Rodríguez-Rodríguez et al. 2021). Some genera of clean waters are characteristic of the upper reaches of rivers, while other genera more tolerant to pollution are located in the middle and lower reaches

density of individual of the three principal subfamilies of chironomids (Tanypodinae, Chironomidae, and Orthocladiinae). However, results also showed that such a pattern changes when considering the number of species. Species richness peak at high- and low-altitude zones, and low values in the middle zone. Likewise, both species richness and density of individuals of each subfamily responded differently to the altitudinal gradient.

5.3 Trophic Structure and the Gradient of Elevation

Biotic factors can drive the altitudinal shifts in macroinvertebrate diversity. Differences in climate, soil, and vegetal coverage – linked to altitudinal gradients (Chap. 1), may alter trophic dynamic in freshwater habitats (e.g., Vannote et al. 1980; Luque-Moreno and González-Trujillo 2021) and in turn modify the trophic relationship that are established between the species and the sources of a food web. Changes in the consumption (prey-predator) relationships, for instance, is one of the interspecific relations more studied between organisms, as it could alter the “ecosystem equilibrium” through the local extinctions due to specific relations as the competition (Tokeshi 1999).

The evaluation of trophic networks is based on their attributes or properties, which allow a comprehensive understanding of the community structure based on the relationship of resources with consumers, interactions of top-predators, and the percentage of omnivores. In this section, we review the studies on the food webs of aquatic invertebrates performed along an altitudinal gradient of the Gaira River in the SNSM. These studies showed that changes in the structure of trophic networks are associated with elevation (e.g., Tamaris-Turizo et al. 2018). For example, the link density (L/S), which is a property associated with the complexity and stability of the ecosystem (Dunne et al. 2002), decreased according to elevational gradient (L/S at low: 4.33; middle: 2.17; and high-altitude: 2.48).

Trophic networks may also exhibit some degree of seasonality along altitudinal gradients. In relation to the trophic species richness, Tamaris-Turizo and colleagues found a lower variability along of the altitudinal gradient during the dry season (low basin: 33; middle sector: 32; highwaters: 31); conversely, in the rainy season the values lowered in all sectors (low basin: 22; middle sector: 24; highwaters: 17). The trophic level and the maximum length of the chain had similar values along of gradient (between 2.83 and 3.13). The fraction of top predators (*t*) displayed a wide variation, so in the lower sector was 0.29 in the rainy seasons and 0.58 in the dry season. In this site, intermediate taxa (mid-network species) had a fraction of 0.27 during the dry season and 0.41 in the rainy season. Diet discontinuity (D_{diet}) is another important property of the trophic networks that permit to know whereas a consumer’s diet is constrained by its phylogenetic origin. In the Gaira River, D_{diet} decreased simultaneously with the decrease in the elevational gradient (Table 5.1), which indicates that the taxonomic relations are stronger in the headwater of the fluvial system, which is associated with recent events of divergence. Other attributes

Table 5.1 Trophic networks properties along an altitudinal gradient in the Gaira River, north of Colombia

Property	High	Middle	Low
Frac. Omnivory	0.19	0.12	0.69
D_{diet}	0.10	0.06	0.02
Resource	15	15	14
Consumer	26	27	28

such as the fraction of omnivores and the number of consumers showed higher values in the sectors of middle and lower elevations and low records in the upper river basin. The vulnerability was low in the rainy season in the middle and upper sections, but increased according to the elevation gain. The vulnerability values of the main food resources decreased downstream. The trophic network data of the Gaira River show that the precipitations could be a factor modulator of disturbs that can produce shifts in some trophic properties (Figs. 5.3 and 5.4).

5.4 Anthropogenic Altitudinal Gradients

While the joint effect of the water temperature and oxygen availability explains to a great extent the altitudinal shifts of aquatic insects (see Jacobsen 2020), recent evidence suggests that other factors may also drive community organization in montane streams. In this section, we will discuss two of them: the anthropic drivers linked to land use changes; and the historical drivers linked to past climatic (e.g., temperature oscillation) and geological (e.g., mountain uplift) events.

Human-origin stressors have differential effects on aquatic ecosystems, which make it difficult to identify whether the structure of a certain biotic community is influenced by altitudinal gradients or by human impacts (Forero-Céspedes et al. 2016; de Paiva et al. 2021). As seen in previous sections, in which the altitudinal gradients of some groups of aquatic insects of Andean streams were mentioned, the structural changes in invertebrate communities intersect with the effects derived from human activities. In this way, the gradient of deterioration of the water is overlaid on the altitudinal gradient, which makes it challenging to establish the natural variation of macroinvertebrate communities. In the specific case of dipterans, the works of Cuadrado et al. (2019) and Rodríguez-Rodríguez et al. (2021) showed that the altitudinal gradients of the rivers they studied coincided with the pollution gradients, which means that the higher the elevation, the better the water quality. Therefore, the greater contamination evidenced at the middle section of the basins could function as an isolation mechanism between the high and low sections, and this seems to reduce both the probability of dispersal of taxa between sites and, subsequently, drive species turnover headwaters

Contrasting results have been found in other studies focused on the effects of human activities on aquatic macroinvertebrates. Meza-Salazar et al. (2020) observed

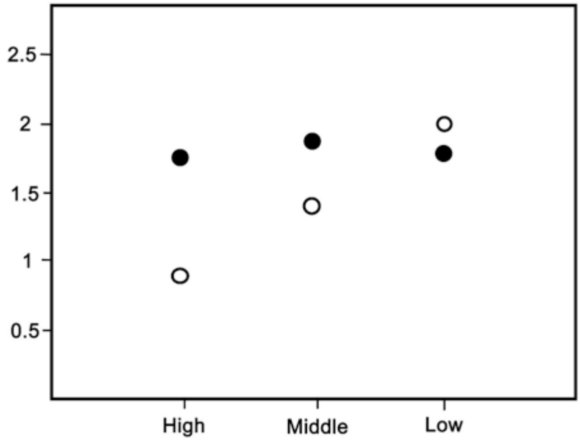

Fig. 5.3 Vulnerability values of a trophic network along their altitudinal gradient during rainy (white circles) and dry seasons (black circles)

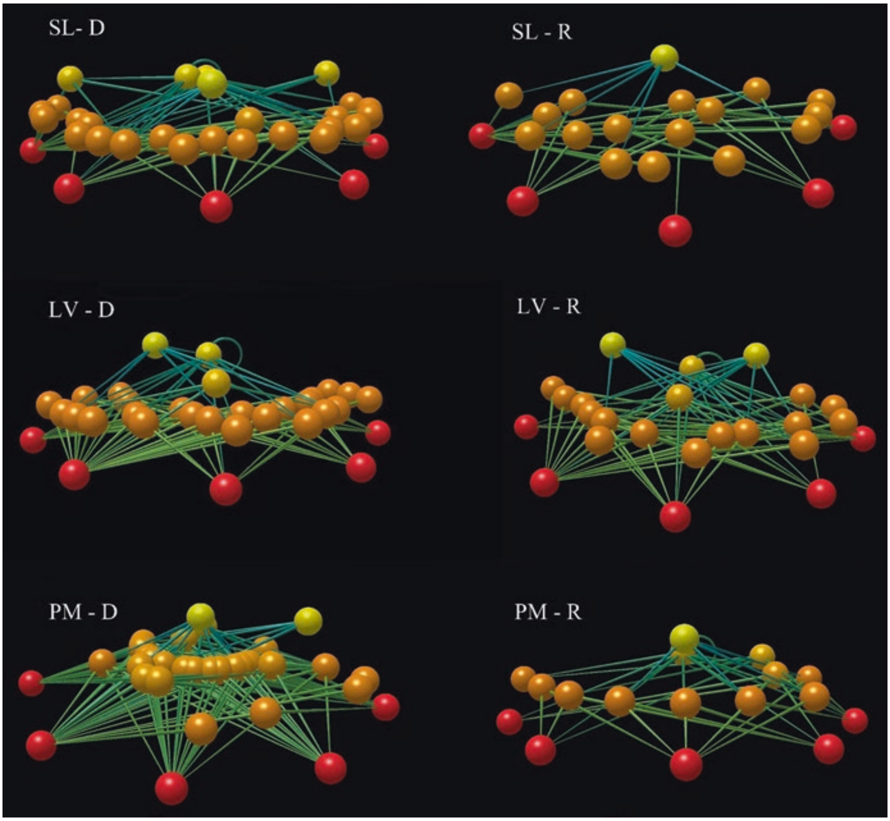

Fig. 5.4 Models of trophic networks at three sites in the Gaira River. Red circles indicate basal resources, orange red intermediate consumer, and yellow circles the top predators. SL San Lorenzo, upper sector; LV La Victoria, middle sector; PM Puerto Mosquito, lower sector; D dry season; R rainy season. (Adapted from Tamaris-Turizo et al. 2018)

in the Caldas Department (Central Mountain Range of Andes) that agriculture has a strong effect on the invertebrate community, causing lower organisms' density and diversity, the dominance of *Simulium*, and the absence of pollution intolerant taxa, such as *Anacroneuria*, *Marilia* (Trichoptera: Odontoceridae), and *Camelobaetidius* (Ephemeroptera: Baetidae). For these authors, this effect of agriculture was even more intense than that produced by livestock or mining. Apparently, in this region of the central Andes of Colombia, mining and agricultural activities are highly variable in their intensity and use of chemical substances, which make it difficult to separate their effects from those dependent on natural hydrological patterns. However, in that study, it was evident that the reference stations, located at a higher elevation (1720 and 2766 masl), and with less anthropic intervention, were more diverse, had a higher abundance of invertebrates, and presented clean water taxa such as *Smicridea* (Trichoptera: Hidropsychidae), *Andesiops* (Ephemeroptera: Baetidae), and *Nanomis* (Baetidae). In addition to the lower degradation by human activities, the presence of riparian forest at these reference sites seems to be one of the reasons for the better conditions of their macroinvertebrate communities.

5.5 Other Drivers Underlying Altitudinal Gradients

As in plant communities, most communities in montane rivers exhibit a high degree of species turnover along elevation gradients (i.e., Wang et al. 2012; Bishop et al. 2015). Such a turnover, as described throughout this chapter, can be explained by the elevation-driven environmental gradients that occur from the bottom to the top of the mountains (Bertuzzo et al. 2016; Nottingham et al. 2018). However, recent evidence has pointed that such a pattern is also shaped by the historical background of the mountain chain (González-Trujillo et al. 2021), at least in the Neotropical region.

In Neotropical basins, past geological and climatic events have a pervasive influence on the contemporary structure of river networks and species distribution (Albert et al. 2018; Bicudo et al. 2019). Andean uplifts and glacier retreats, among others, have shaped unique combinations of river forms and riparian ecosystems at the ecoregional scale in the Orinoco and Amazonas River basins (Rull 2008; Bicudo et al. 2019). Thus, when descending from the Andes to the Amazon, there is a matrix of streams with constrained channels that are surrounded by shrubs in the Paramo, followed by rivers with gorge channels and steep slopes in the Andean-cloud Forest and Piedmont regions, and then meandering rivers surrounded by well-developed rainforest in the Amazonian region. As such, an ecoregional gradient is presented that is coupled with the elevational gradient.

Recent studies have shown that the distribution of diatom and invertebrate taxa partially follows the distribution of ecoregions within the basin (Fig. 5.5) (González-Trujillo et al. 2020a, b). Regardless of their spatial proximity, diatom and invertebrate communities from streams within the same ecoregions were more similar to each other than to those from different ecoregions. Besides, both the environmental features and the species composition of communities in every stream were

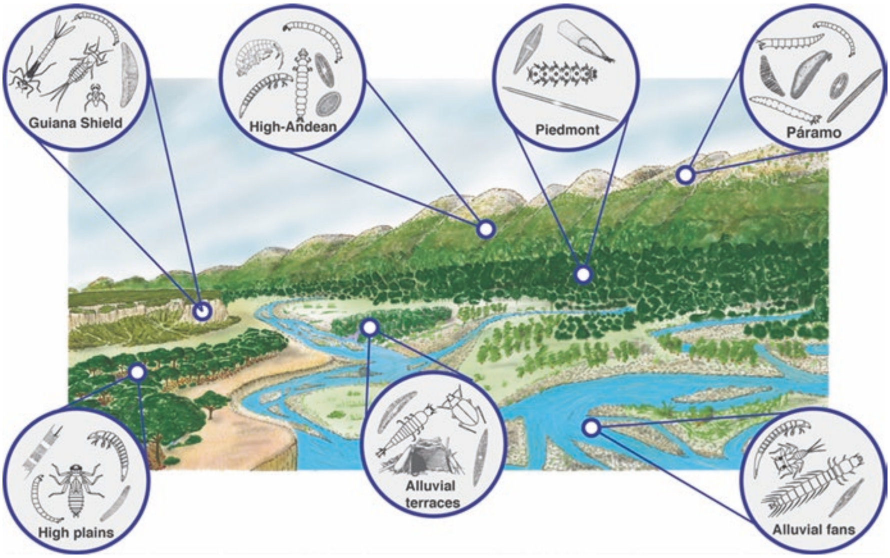

Fig. 5.5 Conceptual scheme representing the ecoregionally constrained distribution of species pools in the Andean mountains

constrained by the type of ecoregion. These patterns suggest the precedence of historical processes over local or regional processes in shaping the contemporary structure of algae and invertebrate metacommunities.

Distributional patterns of diatoms and invertebrates across the Orinoco indicate that knowing the historical background of a region is essential to gain a better understanding of the mechanisms supporting metacommunity-level patterns. Metacommunity ecology needs to embrace biogeography and integrate geological and climatic history with statistical tools. Indeed, a reconstruction of the evolutionary history of the Colombian Andes provides evidence supporting that those past historical events have contributed to shaping the present-day diversity and distribution of benthic communities; and especially, that historical events seemed to be essential in separating lineages (and taxa) in different ecoregions regardless of the long time available for dispersal (thousands or millions of years) (González-Trujillo et al. 2021).

However, historical legacies cannot be fully disentangled from environmental contemporary effects. A different number of present-day factors can also significantly explain the distribution of species along altitudinal gradients (González-Trujillo et al. 2021). While this may serve as evidence supporting that species distributions respond to the environmental changes along the altitudinal gradients, the effect of the environment is not interpretable without considering the historical background of the basin. Historical legacies may constrain the variability of some environmental factors, such as stream water pH, temperature, or substratum mobility. Temperature, for instance, is majorly driven by the altitudinal ranges of

Neotropical mountains (Gill et al. 2016). Substratum mobility, on the other hand, is highly dependent on the fluvial landform (Stallard 1985). Therefore, in line with Perrigo et al. (2019), recent findings emphasize that montane geology sets the stage for speciation and landscape formation, where different ecological and environmental factors co-act to increase biodiversity. As such, altitudinal gradients in the Tropics should be addressed considering both historical and contemporary factors, without excluding the effect that humans have on streams and rivers.

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