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Habitat preferences and simulation of physical habitat availability of Perlidae (Plecoptera) and Corydalidae (Megaloptera) in a neotropical river

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ABSTRACT

Introduction: Habitat preferences represent the distribution and abundance of species among different habitat types. These preferences are highly relevant ecological information because they relate to the feeding strategies, offspring care and predator avoidance refuges of the organisms, therefore potentially influencing their fitness.
Objective: To define the habitat preference of the nymphs of *Anacroneuria* spp. (Plecoptera) and larvae of *Corydalus* spp. (Megaloptera) with respect to current velocity and depth.
Methods: We evaluated the abundance of *Anacroneuria* and *Corydalus* with information gathered through 15 field campaigns in three sites of the Savegre River, Costa Rica. Also, we used habitat preferences to create simulations of the physical habitat availability for these species through hydraulic models to determine habitat gain or loss due to variations in flow.
Results: *Anacroneuria* (Plecoptera) nymphs preferred velocities of 0.9 m/s and depths between 23-36 cm, while *Corydalus* (Megaloptera) larvae preferred velocities between 0.6-0.8 m/s, and depths between 17-29 cm. As a case study, these preferences were modeled to determine optimal, regular or inadequate habitat availability for *Anacroneuria* and *Corydalus* given hypothetical flow variations in the Savegre River (Costa Rica). A discharge of $< 8\ m^3/s$ resulted in a decrease in optimal habitat, mainly because it decreased water velocity below the preferred ranges. Also, a discharge of $> 18\ m^3/s$ resulted in a decrease in optimal habitat because of the depth increase.
Conclusions: This type of information is scarce or even absent for neotropical rivers, though necessary for a description of a healthy habitat. Furthermore, this habitat preference vs. modeled habitat availability approach is highly useful, -both in tropical and temperate rivers- for understanding the potential effects of any water derivation or exploitation.

Key words: aquatic insects; stoneflies; dobsonflies; hydrobiological model; river management.

RESUMEN

Preferencias de hábitat y simulación de disponibilidad de hábitat físico de Perlidae (Plecoptera) y Corydalidae (Megaloptera) en un río neotropical

Introducción: Las preferencias de hábitat representan la distribución y abundancia de las especies entre distintos tipos de hábitat. Estas preferencias constituyen información ecológica de gran relevancia ya que están relacionadas con las estrategias de alimentación, el cuidado de las crías y los refugios para evitar la depredación, por lo que pueden influir en su supervivencia y capacidad reproductiva.

Objetivo: Definir la preferencia de hábitat de ninfas de *Anacroneuria* spp. (Plecoptera) y larvas de *Corydalus* spp. (Megaloptera) con respecto a la velocidad de la corriente y la profundidad.

Métodos: Con información recopilada a través de 15 campañas de muestreo en tres sitios del río Savegre, Costa Rica, se evaluó la abundancia de *Anacroneuria* y *Corydalus*. Además, las preferencias de hábitat de las especies se utilizaron para crear simulaciones de la disponibilidad física de hábitat mediante modelos hidráulicos y determinar la ganancia o pérdida de hábitat debido a variaciones en el caudal.

Resultados: Las ninfas de *Anacroneuria* (Plecoptera) prefirieron velocidades de 0.9 m/s y profundidades entre 23-36 cm, mientras que las larvas de *Corydalus* (Megaloptera) prefirieron velocidades entre 0.6-0.8 m/s y profundidades entre 17-29 cm. Como estudio de caso, se modelaron estas preferencias para determinar la disponibilidad de hábitat óptimo, regular o inadecuado para *Anacroneuria* y *Corydalus* dadas las variaciones hipotéticas de caudal en el río Savegre (Costa Rica). Un caudal < 8 m^3/s resultó en una disminución del hábitat óptimo, principalmente debido a la disminución de la velocidad del agua por debajo de los rangos preferidos. Asimismo, un caudal de > 18 m^3/s provocó una disminución del hábitat óptimo debido al aumento de la profundidad.

Conclusiones: Este tipo de información es escasa o incluso inexistente para los ríos neotropicales, aunque necesaria para la descripción de un hábitat saludable. Además, comparar la preferencia de hábitat frente a la disponibilidad de hábitat modelada es muy útil -tanto en ríos tropicales como templados- para comprender los efectos potenciales de cualquier derivación o explotación de agua de un cauce.

Palabras clave: insectos acuáticos, moscas de la piedra, megalópteros, modelo hidrobiológico, gestión fluvial.

INTRODUCTION

Aquatic macroinvertebrates constitute a diverse community of organisms that have been extensively utilized for biomonitoring purposes over the past several decades (Bonada et al., 2006, Sumudumali & Jayawardana, 2021). These organisms are a vital component of aquatic ecosystems, representing approximately 60 % of the animal biodiversity in continental freshwater environments (Balian et al., 2008). Additionally, macroinvertebrates play essential roles in energy transfer, aquatic trophic dynamics, and nutrient cycling, both within aquatic ecosystems and in the adjacent terrestrial environments (Dijkstra et al., 2014). Among aquatic macroinvertebrates, insects form the largest group and, although they have been relatively well studied, significant gaps in basic ecological knowledge persist (Hauer & Resh, 2002; Starr & Wallace, 2021). These knowledge gaps limit the full potential of aquatic insects as tools for decision-making processes and watershed management.

Habitat preferences describe the distribution and abundance of species across different habitat types, enabling the identification of the most characteristic habitats (Baptista et al., 2001). This ecological information is highly relevant, as it is closely linked to feeding strategies, offspring care, predator avoidance, and the availability of refuges, and environmental tolerance, all of which can significantly influence the fitness of organisms. Furthermore, understanding habitat preferences provides valuable insights for predicting how species might respond to habitat loss (Beyer et al., 2010).

In lotic systems, habitat preferences are typically represented as preference curves or habitat suitability curves, which are used to assess the quantity and quality of available habitat in relation to river flow (Kelly et al., 2015; Shearer et al., 2015; Theodoropoulos et al., 2015; Vázquez et al., 2020). These preference curves can also be employed to generate simulations of physical habitats using eco-hydraulic models, which facilitate the evaluation of habitat gain or loss in response to flow variations (Im et al., 2011; Im et al., 2018; Kim & Choi, 2018), whether these variations are of natural origin or result from anthropogenic activities, such as hydropower dams or irrigation reservoirs.

Ecological information, habitat preferences and eco-hydraulic modeling of aquatic species sensitive to changes in discharge can be used to calculate environmental flows for rivers where water extraction or derivation is contemplated.

Such sensitive species information (bioindicators) is important to assure the biodiversity and ecological integrity of rivers subjected to human activities (Chaves et al., 2010). Until now, almost all flow bioindicator species used worldwide have been fish (Theodoropoulos et al., 2018), which render valid information, but are difficult to sample or quantify, and are also limited in their altitudinal distribution (e.g. no native fish species exist in Costa Rica above 1 400 m a.s.l; Angulo et al., 2013). This created the need for additional biological data derived from other ecologically relevant groups of aquatic biota in rivers (Chaves et al., 2010; Vázquez et al., 2020). Moreover, Kelly et al. (2015) questioned the applicability of generalized habitat suitability curves across diverse river systems, underscoring the need for region-specific data, particularly for neotropical species and rivers.

For this research, we selected nymphs of the aquatic insects *Anacroneuria* (Plecoptera: Perlidae) and larvae of *Corydalus* (Megaloptera: Corydalidae) as study organisms. The nymph and larvae of both orders are typically associated with riffle areas with fast flowing and well-oxygenated habitats (Quesada-Alvarado et al., 2021), as well as to litter and rocky substrates (Baptista et al., 2001; Tamaris-Turizo et al., 2007). They also have a bigger size than other aquatic insects, are easy to recognize in field samples and have a low number of described genera and species in the Neotropics, which makes the taxonomic identification process more straightforward (Bravo et al., 2019; Gutiérrez-Fonseca et al., 2015; Stark, 2014). Both genera are considered sensitive to water pollution and alteration (Luiza-Andrade et al., 2022; Rico & Van den Brink, 2015). Due to their ecological requirements, both can be used as sentinels for environmental changes, mainly because they require high concentrations of dissolved oxygen and, as predators, they rely on a diverse prey community (Rivera-Gasperín et al., 2019). Therefore, it is necessary to gain knowledge about their ecological requirements in terms of simple hydraulic variables such as water velocity and depth, which can help establish baselines for climate change scenarios, possible hydrological changes in watersheds, as well as alterations in flow caused by hydroelectric projects or water extraction.

Only recently has research begun to link hydraulic variables with macroinvertebrate taxa in this region (Quesada-Alvarado et al., 2020; Quesada-Alvarado et al., 2021; Vázquez et al., 2020; Chavarría-Pizarro el at., 2024). Our study contributes to this effort following the approach of Quesada-Alvarado (2021), by combining expert panel input and field measurements to develop preference curves for two vulnerable native genera of aquatic insects, *Anacroneuria* spp. (Plecoptera: Perlidae) and *Corydalus* spp. (Megaloptera: Corydalidae), in a neotropical Costa Rican river (Savegre). We further demonstrate their application through a case study modeling optimal environmental flow based on ecohydraulic data and the habitat preferences developed in this study. This approach is useful for understanding the potential effects of water derivation or exploitation in tropical and temperate rivers.

MATERIALS AND METHODS

Study area and sampling: The study was executed in the Savegre River watershed, located in Costa Rica´s Pacific slope (9°34´-9°63´ N & 83°71´-84°07´ W; SMF1). The elevation in this watershed ranges from 0 to 3 491 m a.s.l., and the annual precipitation varies from 3 000 to 7 000 mm, with a dry season between December and April, and a rainy season between May and November (Espinoza-Cisneros, 2021). This watershed comprises 600 km^2, has an average flow of 9.7 m^3/s in the driest periods, and 98.3 m^3/s in the peak of the rainy season (according to data from this study).

The sampling was executed during the rainy (May-November 2011) and dry seasons (January-April 2012) with a total of fifteen field campaigns at three sites along the Savegre river. The sites have riverside forests on both margins and are in a very humid premontane forest, according to the Holdridge (1964) life zones classification. Table 1 summarizes some general characteristics of each site studied.

Table 1
Location and characteristics of the study sites of Savegre River.

	Site 1 (S1)	Site 2 (S2)	Site 3 (S3)
Location	N 9º 27’431” - W 83º58’389”	N 9º 27’707” - W 83º58’560”	N 9°26’ 939” - W 83°59’531”
Elevation	250 m.a.s.l.	294 m.a.s.l.	112 m.a.s.l.
Substrate	boulders and cobbles	boulders and gravel	boulders and gravel
Vegetation of the riverbank	trees and shrubs	trees, shrubs and grasses	trees, shrubs and grasses

At each site during each field campaign, a 50 m section of the river was used for the collection of nymphs of *Anacroneuria* and larvae of *Corydalus*. A total of 12 samples (12 replicates per site) were collected monthly; these samples were taken in different water current velocities (assessed by means of a flowmeter Flow Watch, FW450) to evaluate the distinct velocity microhabitats offered by the river. At each one of these microhabitats, depth was also determined, and then a D-net (500-µm pore) was introduced to sample macroinvertebrates. The substrate was removed for 30 seconds to collect the organisms in the net. The sample material was deposited in white trays *in situ* and the nymphs and larvae were separated and preserved in vials (8.0 x 3.0 cm) with ethanol 85 %. Larger *Corydalus* larvae (≥ 4 cm) were not preserved, only measured *in situ* and returned to the river once sampling was completed. In the laboratory, the identification of *Anacroneuria* species was carried out using Gutiérrez-Fonseca and Springer (2011), while for *Corydalus*, Contreras and Harris (1998) was used. Size (body length; mm) was also recorded with a ruler for *Corydalus* because changes in habitat selection have been documented according to larval stage. At each microhabitat evaluated, dissolved oxygen (mg/l), temperature (°C) and distance to the river edge (m), were also measured with multiparameter equipment (Extech DO700) and a measuring tape, respectively. The collection of both larvae was carried out under permit number 121-2011-SINAC granted by the National System of Conservation Areas (SINAC) of the Ministry of Environment and Energy (MINAE) of Costa Rica.

Habitat preferences: To elucidate the habitat preferences, an expert panel was consulted to determine velocities and depths at which the nymphs of *Anacroneuria* and the larvae of *Corydalus* are usually registered (Chaves et al., 2006). With this information, a baseline was generated for each order to compare later with data acquired in the field.

The velocity and depth preferences were classified following the fuzzy logic theory, which assumes that complex systems are characterized by imprecise transitions between different states of a system. Fuzzy logic allows the system to have intermediate states since transitions in ecology are gradual, not sharp (Noack et al., 2013). Therefore, three categories of habitat are generated according to the abundance distributions of the organisms and following the fuzzy logic theory to assign the preference: *Optimal*, where the species is very likely to be present as the habitat has the preferred conditions of velocity or depth; *Regular*, where the species can be found, but in lower abundances; and *Inadequate*, where conditions of water velocity and depth are not favorable and finding the species is unlikely.

The fuzzy rules, as mentioned above, generate overlapping classes (fuzziness). However, to classify any value of depth and current velocity into a specific category of habitat preference (optimal, regular or inadequate), membership functions are calculated. The membership functions are usually represented by simple trapezoidal or triangular functions that are expressed from 0.0 to 1.0, where 0.0 indicates that the values of the variable are not part of the category, and 1.0 indicates that the values are entirely part of the category (Noack et al., 2013).

Data Analysis: The water velocities measured in the field were classified in three categories: low (< 0.4 m/s), moderate (0.4 to 1 m/s) and fast (> 1.01 m/s) using Extence et al. (1999); while the depth was categorized in 10 cm ranges. This was done to ensure replicability, given the wide range of depths and based on the premise that similar hydraulic conditions can be maintained within each 10 cm interval.

We used PERMANOVA tests, using a Bray-Curtis dissimilarity matrix and 999 permutations, to determine differences in velocity and depth preferences of *Anacroneuria* species (PERMANOVA test did not apply to *Corydalus*, as the larvae are difficult to identify at the species level and there are no available taxonomic keys for this purpose). The abundances of *Anacroneuria* and *Corydalus* were log-transformed and a Shapiro-Wilk test was applied, due to the non-normality of the data a Kruskall Wallis test was performed, we calculated the effect size (epsilon square) for the tests that were significant. With the subsequent post hoc Dunn's test we determined if the abundance was different between velocity categories or depth ranges. To understand the relationship between velocity and larval abundance, a Generalized Additive Model (GAM) and a Linear Model (LM) were first compared using their AIC values. The AIC of the GAM was lower than that of the LM, indicating nonlinearity in the data. However, when analyzing the quantile plot of the GAM variance residuals, residual overdispersion was observed due to the number of zeros present in the data. Due to the high frequency of zero counts in the dataset, we fitted a zero-inflated Poisson (ZIP) model. The model includes a count component (Poisson) and a zero-inflated component (binomial). The two models, ZIP and GAM, were compared using the log-likelihood value.

We also conducted a log-linear regression (LLR) to explore the relationship between the distance from the riverbank and body size of *Corydalus* larvae. We used LLR because we observed an exponential decrease in *Corydalus*' body size. This analysis was carried out only for *Corydalus* since these larvae have the behavior of burying themselves in the riverbank to carry out their metamorphosis, so larvae could change their habitat preference according to their growth and larval maturation.

These analyses were performed with R programming environment and language (R Core Team, 2024), and using the package vegan (Oksanen et al., 2020), mgcv (Wood, 2017) and pscl (Jackman, 2020).

We did not use the environmental variables (DO, pH and others) as predictors of habitat selection, we used them as controls to determine whether the presence/absence was due to water quality conditions or habitat quality. For this reason, we did not apply statistical methods to them.

Case Study, habitat availability: The Costa Rican Institute of Electricity (ICE), developed a holistic methodology and software named "RANA" (Chaves et al., 2006; Chaves et al., 2010; Laporte et al., 2006) to determine appropriate environmental flows according to socio-economic, hydrologic and biological data (fish, macroinvertebrates and amphibian -flow indicator species), with the aim of reducing the impacts of dams on ecosystems and communities (Chaves et al., 2006; Chaves et al., 2010). This methodology allows processing and data analysis regarding the habitat preferences of bioindicator species (in this study *Anacroneuria* and *Corydalus*), to propose an environmental flow that considers the ecological requirements of the most sensitive species. RANA also produces a graphical visualization of the velocities and depths of a river stretch, making it possible to see what portions of the river stretch would be restrictive to the flow indicator species (in terms of current velocity or depth). We used the RANA software to create the *Anacroneuria* and *Corydalus* habitat availability models. For more information about the RANA methodology, the reader can access the Toolkit for environmental flows at the United Nations Educational, Scientific and Cultural Organization website (The United Nations Educational, Scientific and Cultural Organization, 2017).

Within RANA, the ecological requirements are expressed using the fuzzy logic approach because it is impossible to establish precisely the range limits to optimal, regular or inadequate conditions. For each variable (current velocity and depth), a fuzzy number for optimal, regular, or inadequate conditions is defined. Each fuzzy number represents a set of values of one variable. Each value in that set (horizontal axis) has an associated degree of membership that is expressed by a value in the interval [0-1] (vertical axis), where 0 indicates no membership and 1 indicates total membership (Noack et al., 2013).

In the same way, a diffuse rule consists of arguments combined by logical operators which conform to a logic expression, and which have an associated consequence, e.g. given that A1 and A2 exist, then B is the consequence. Therefore, in the construction of diffuse rules some premises need to be established; in this study, premises about velocity and depth will generate different responses from optimal to inadequate. The applicability is a non-binary function, where the response is a degree of fulfillment (DOF) also expressed by a value in the [0-1] interval. DOF is a value that corresponds with the conditions given by the rule premises.

RANA methodology uses the minimum combination to calculate the condition (optimal, regular, or inadequate) for a specific point in the river based on the associated category of flow velocity and depth. The result corresponds to the lower category obtained in evaluating the value of each premise according to the fuzzy numbers associated with them. For example, if we evaluate flow velocity 0.1 m/s and depth of 1 cm, the result is "inadequate" with DOF = 1, because 0.1 m/s has a degree of membership of 1 for inadequate, and 1 cm depth has a degree of membership of 1 for optimal, then the result condition is inadequate, which is the lower category.

For this study, stretch S1 (Fig. 1) was used to evaluate ecological constraints (habitat preferences) for *Anacroneuria* and *Corydalus*. We used the simple hydraulic model generated by the hydraulic module of RANA software to evaluate the fulfillment of the ecological

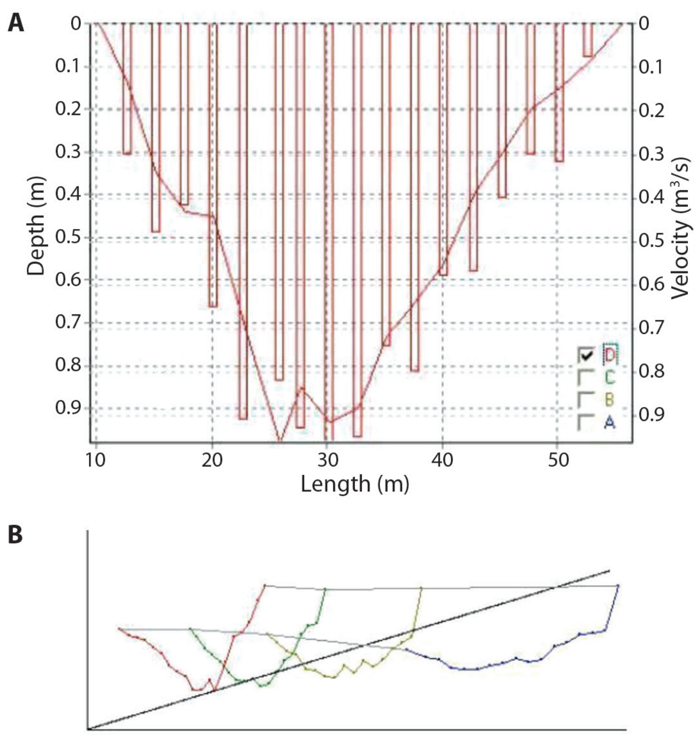

Fig. 1. Scheme of the stretch S1. **A.** Cross-sectional view. **B.** three-dimensional view. From Krasovskaia & Rodríguez (2007).

requirements at this point. The hydraulic model allows us to obtain simulations for different water discharges. The simulations provide a set of points in the stretch for which we have the x, y, and z arbitrary coordinates (to generate visualizations) and the flow velocity and depth (to evaluate the habitat preferences).

RANA software evaluates the ecological constraint for each simulated point in the site of interest and produces a graphical visualization of resulting conditions evaluation, using green for each point that has optimal habitat for the flow-indicator species, yellow for regular habitat and red for inadequate habitats. The most restrictive value (lowest category) is assigned when flow velocity and depth evaluation are combined for each point. For example, in each case where flow has an inadequate condition, but velocity has a regular or optimal condition, the simulated point in that site would be assigned inadequate (red). Furthermore, RANA calculates the amount of optimal, regular and inadequate habitats for any user-given flow included in the simulations.

RESULTS

Habitat preferences: The expert panel (composed of six experienced aquatic entomologists) indicated that stoneflies and dobsonflies are rheophiles with a preference for moderate and high current velocities. They also considered Perlidae to be the family with the greatest demand for high velocities. In terms of depth, they indicated that Perlidae and Corydalidae could live in shallow waters and up to a depth of 1.8 m (Table 2).

For the Savegre river watershed, registered variables in each study site (15 sampling campaigns) are described in Table 3. The maximum velocity recorded was obtained in a microhabitat composed of rock and at a shallow depth, allowing an increase in water velocity. The maximum flow was recorded during the month of October, which is the month with the highest rainfall in Costa Rica´s Pacific slope, while the minimum flow was recorded during the month of March, which is the peak of the dry season.

In total, 194 macroinvertebrate samples were processed and 179 individuals of four different species of the genus *Anacroneuria* were collected (*A. marca, A. benedettoi, A. holzenthali* and *A. perplexa;* Plecoptera: Perlidae). There was no difference in the water velocity preference between these four species (Permanova = 1.53; p = 0.77). All *Anacroneuria* nymphs were found in habitats with velocities between 0.5 to 1.8 m/s. Moreover, as velocity increased, the abundance of organisms increased, reaching a peak between 0.6 and 1.2 m/s, and after that,

Table 2
Velocity and depth preferences of Perlidae and Corydalidae for Costa Rican rivers (Theoretical rule: according to the opinion of the experts panel).

Classification of habitat	Velocity (m/s); theoretical rule		Depth (cm); theoretical rule	
	Anacroneuria	*Corydalus*	*Anacroneuria*	*Corydalus*
Optimal	1.0-5.0	0.4-0.9	0.5-1.7	0.2-1.8
Regular	0.3-1.2	0.2-0.4; 0.8-1.2	0.1-0.05; 1.4-3.1	0.01-0.2; 1.4-3.2
Inadequate	0-0.5	0-0.5; 1.1-2.0	2.7-6	0.1-0.01; 2.7-6.0

Table 3
Summary information of the three study sites, throughout the 15 field campaigns. Savegre river, 2011-2012.

Site	DO (mg/l)		Temperature (°C)		Flow (m^3/s)		Velocity (m/s)		Depth (m)	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
S1	10.3	8.3	24.3	20.6	92.4	9.7	2.13	0	0.93	0.07
S2	8.9	7.5	26.7	21.7	92.4	9.7	1.67	0	0.81	0.13
S3	9.3	7.7	27.9	18.7	98.3	9.9	1.3	0	0.51	0.17

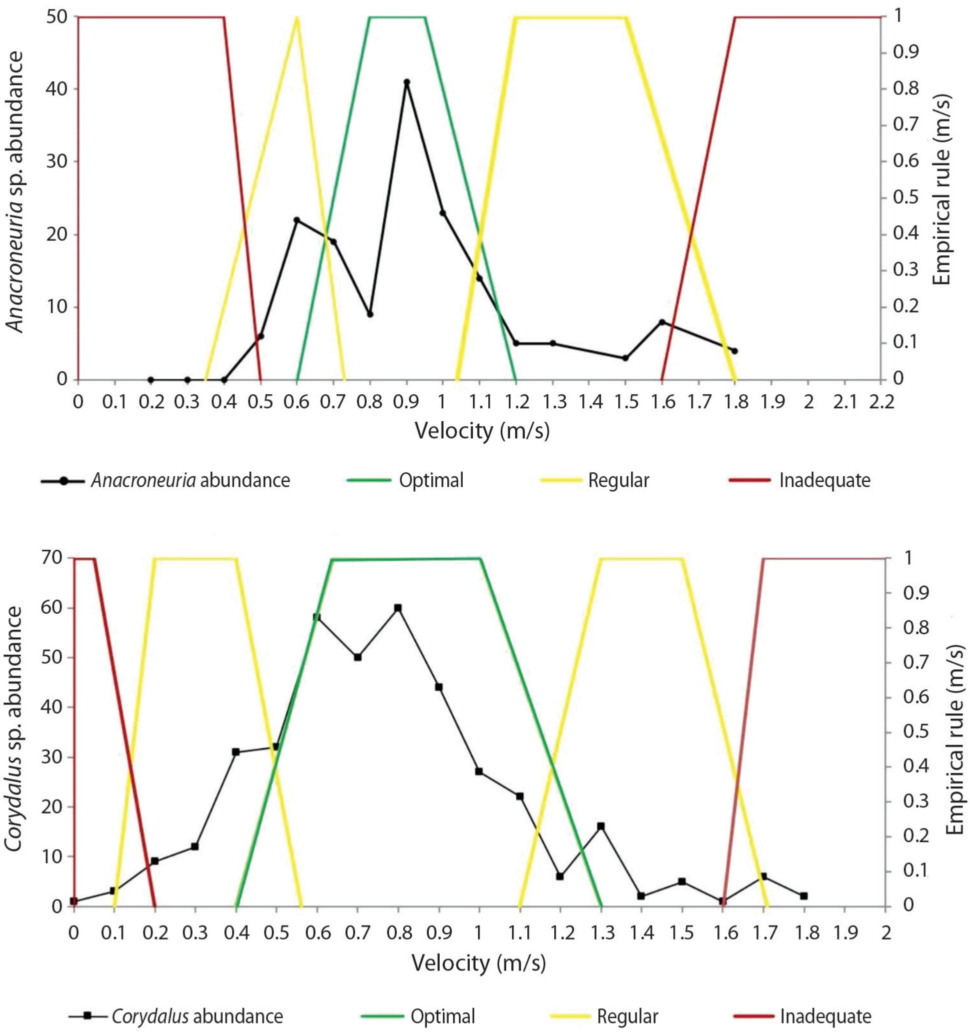

Fig. 2. Fuzzy numbers used to determine optimal, regular and inadequate habitat for *Anacroneuria* nymphs (Plecoptera: Perlidae) and *Corydalus* larvae (Megaloptera: Corydalidae) based on flow velocity in the Savegre River, Costa Rica.

the abundance began to decrease at extreme velocities (> 2 m/s; Fig. 2). A greater abundance of stoneflies was recorded within the moderate and fast velocity categories, in comparison with low velocity (Kruskal-Walis = 15.12; $p < 0.05$; effect size: 0.150). However, there was no difference between moderate and fast velocities (Dunn's test $p > 0.05$). According to the count component of the zero-inflated Poisson model, the expected abundance of Plecoptera increases by approximately 4 9 % for each 1 m/s increase in flow velocity ($\beta = 0.3987$, $p = 0.019$). The intercept ($\beta_0 = 0.6928$) indicates that, in the absence of flow (0 m/s), the expected abundance is around two individuals, assuming the observation is not a structural zero. Therefore, increased water velocity is a factor modulating the abundance of Plecoptera larvae.

It is noteworthy to mention that the DO concentration slightly increased with each velocity category (low: mean DO 8.6 ± 0.6 mg/L; moderate: mean DO 8.8 ± 0.7 mg/L; fast: mean DO 9.1 ± 0.7 mg/L). A similar trend was observed with the preferences of water depth.

Two extremes were found: very shallow (< 10 cm) and deep waters (> 100 cm), both with a reduced number of organisms, while the greatest abundances of stoneflies were found between 23 and 36 cm. However, there was no difference between the depth categories (Kruskal-Walis = 6.05; $p > 0.83$).

For Megaloptera larvae, a total of 97 individuals of the genus *Corydalus* (Corydalidae) were collected. Larvae. were most abundant and frequently found within moderate current velocities (0.5-1.0 m/s), however, we did not find a difference between velocity categories (Kruskal-Wallis = 0.87; p = 0.97; Fig 2). As well as for *Anacroneuria*, there is an increase in abundance with increasing current velocity, until it reaches a maximum point between 0.6 and 0.8 m/s, and then the abundance decreases. The count model indicated a slight but significant negative effect of the velocity ($\beta = -0.333$, p = 0.075), suggesting that abundance may decrease with increasing velocity. The zero-inflation model revealed a significant base probability of structural zeros (logit intercept = -1.600, $p < 0.001$), corresponding to a 17 % probability of excess zeros. This supports the presence of two processes: one generating true absences and another generating counts. In terms of depth, the greatest abundance of *Corydalus* was recorded between 16 and 29 cm, but without a difference with respect to the other depth categories (Kruskal-Walis = 1.04; p = 0.31).

Also noteworthy is the fact that a regression analysis showed that most large-sized *Corydalus* larvae were collected near the riverside, while small larvae were found far from the bank (R^2= -0.64; p = 0.00) (Fig. 3).

With these preferences, the classification of the velocity values into the optimal, regular and inadequate categories, was established. However, preferences were not as clear for depth and, therefore, the opinion of the panel of experts (theoretical rule) was used for the establishment of the categories (Table 4).

Case Study, habitat availability: Habitat availability modeling was carried out using the habitat classification shown in Table 4. Fig. 4 shows the percentile distribution of the optimal, regular or inadequate habitats in Savegre River for *Anacroneuria*, under different flow scenarios (3, 8, 13, 18, 23 and 28 m^3/s). The different flows were modeled in a stretch of 75 m long, named S1. In this application, the most favorable flows for *Anacroneuria* nymphs are those between 8-18 m^3/s, because those are the ones that provide the highest percentage of optimal habitat.

All modeled flows had a predominance of inadequate and regular areas along the first 40 m, since the stretch morphology created low current velocity and deep areas, which are not suitable for *Anacroneuria* spp. nymphs.

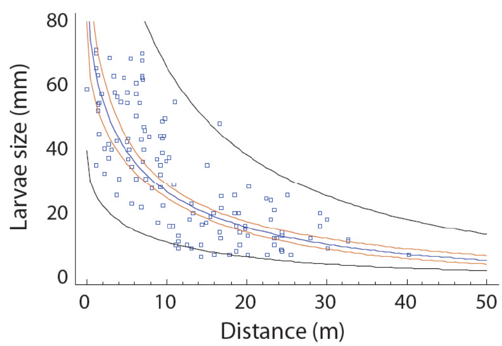

Fig. 3. Relationship between the body size of *Corydalus* larvae and their distance from the riparian forest. The blue line is the Regression line, red lines are lower and upper confidence limit (95 %).

Table 4
Perlidae and Corydalidae velocity and depth water habitat preference in the Savegre River.

Classification of habitat	Velocity (m/s); empirical rule		Depth (cm); theoretical rule	
	Anacroneuria	*Corydalus*	*Anacroneuria*	*Corydalus*
Optimal	0.8-1.2	0.4-1.3	0.5-1.7	0.2-1.8
Regular	0.35-0.73; 1.04-1.80	0.1-0.6; 1.1-1.7	0.1-0.05; 1.4-3.1	0.01-0.2; 1.4-3.2
Inadequate	1.6-3.0	0.0-0.2; 1.6-3.0	2.7-6.0	0.1-0.01; 2.7-6.0

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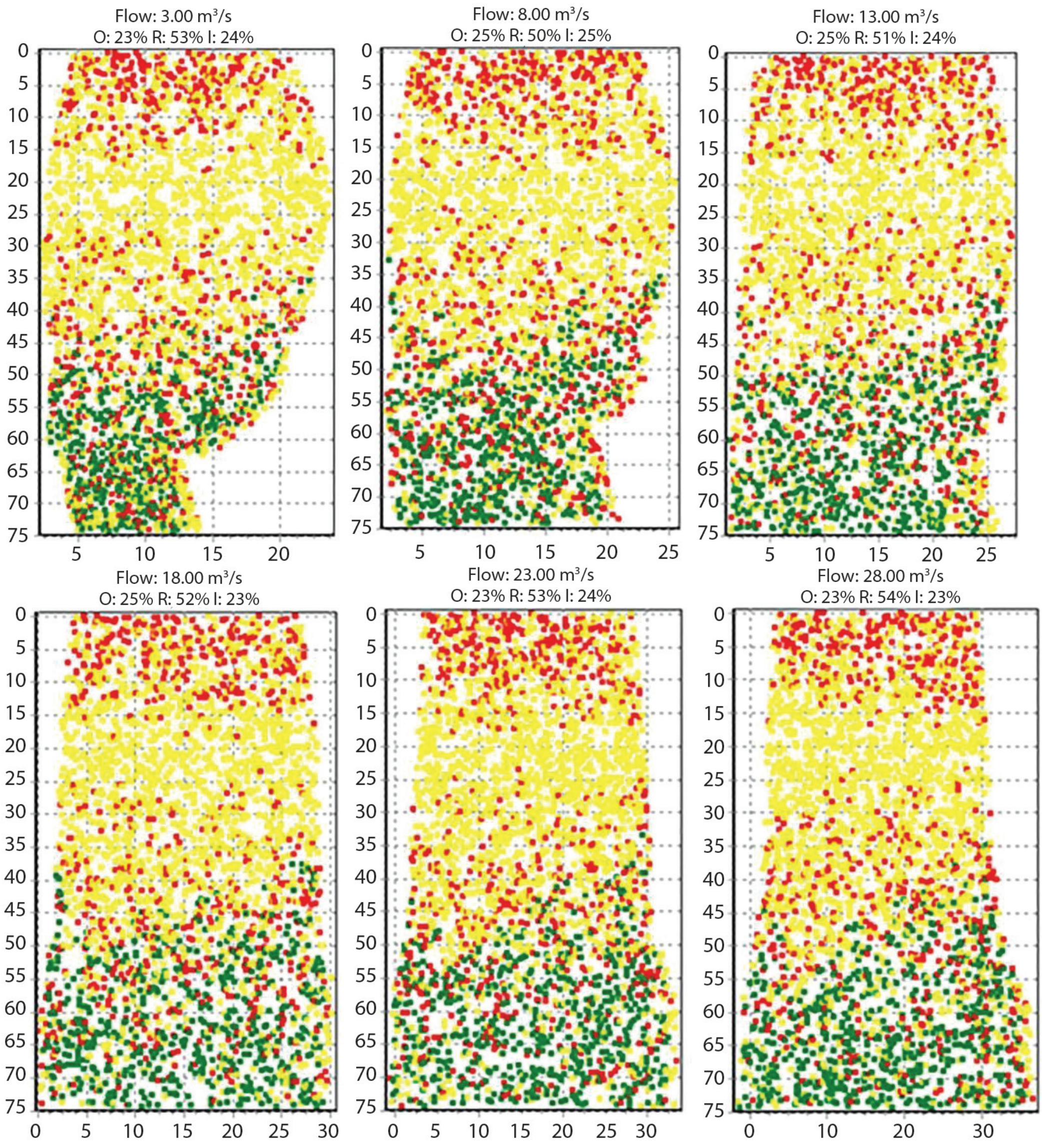

Fig. 4. Above view of the modeled critical dam site of the Savegre River for different flow scenarios. The optimum (green), regular (yellow) and inadequate (red) percentage of habitats for *Anacroneuria* spp. larvae are presented for each modeled flow (The x-axis corresponds to the width and the y-axis to the length of the river stretch).

However, from 45 to 75 m, river morphology changes, creating optimal habitats for the nymphs, with rapids and riffles. Under a flow of 3 m^3/s, the river becomes narrower, and consequently, the area of fast-flowing waters is smaller. With higher flows, fast water areas are increased and so is the availability of habitats for *Anacroneuria* spp. nymphs. However, with flows higher than 18 m^3/s, the percentage of optimal habitats slightly decreases, due to an increase in depth. A flow of 13 m^3/s can be considered as the flow that benefits the larvae of *Anacroneuria* spp., because it generates the set of velocities and depths that the larvae prefer

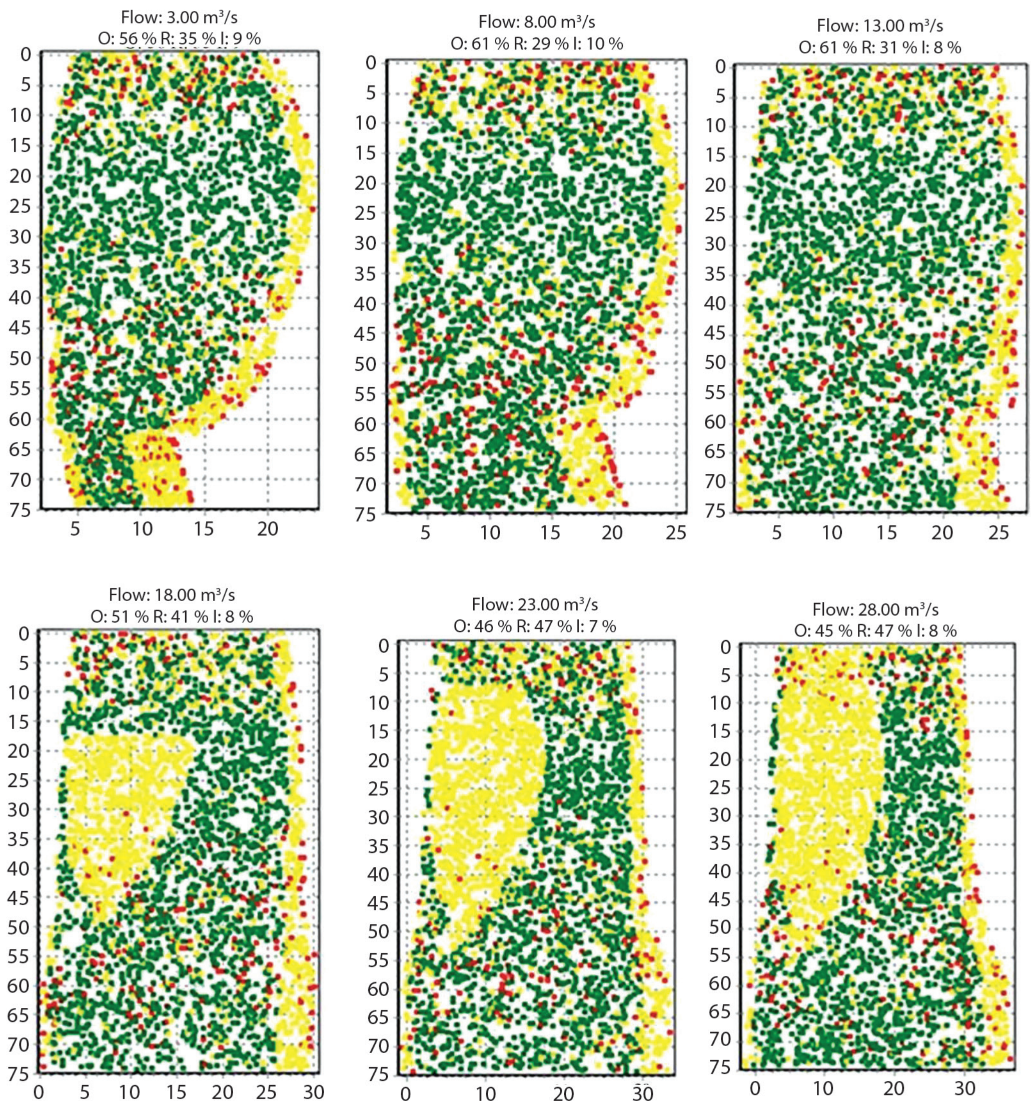

Fig. 5. Above view of the modeled critical Dam site of the Río Savegre for different flow scenarios. The optimum (green), regular (yellow) and inadequate (red) percentage of habitats for *Corydalus* spp. larvae are presented for each modeled flow (The x-axis corresponds to the width and the y-axis to the length of the river stretch).

and, at the same time, the river widens in the most turbulent section, generating a greater supply of optimal habitat.

In the case of *Corydalus* larvae, a 13 m^3/s flow was also the best scenario, since it resulted in the highest percentage of optimal and the lowest percentage of inadequate habitats. As the water volume in the model increased (> 18 m^3/s), the optimal area decreased. However, as the flow increased, the sector of the modeled river stretch increased its width, allowing for higher availability of habitats and more proximity to the riverbank (with ecological advantages because of terrestrial-aquatic ecosystem interactions). In all modeled flows, the percentage of inadequate habitat was lower than the percentages of regular and optimal habitats (Fig. 5).

DISCUSSION

This research demonstrates the affinity of *Anacroneuria* spp. and *Corydalus* spp. for moderate and fast current velocities while also preferring low depths. *Anacroneuria* nymphs and *Corydalus* larvae are known benthic rheophilic organisms with the ability and anatomical traits to colonize areas with fast and turbulent water. They have a dorsoventrally compressed body and hook nails to hold on firmly to the substrate (Stark 2014). In this study, both Perlidae and Corydalidae, preferred habitats where water velocity is considered moderate to strong (0.6-1.8 m/s). It is noteworthy to mention that such velocities influence the presence of certain types of substrates, with dominance of rocks and boulders (Leopold et al., 1992). Therefore, microhabitat preferences related to substrate choice or position of the insects in the benthic zone (over or under rocks or in crevices) are equally related to the velocity regime.

The abundance of both orders increased as velocity increased until a maximum peak was reached, thereafter, the abundance diminished and at velocities higher than 2 m/s, none of the orders were found. Waddle & Holmquist (2011) found the same relation regarding the % EPT (Plecoptera, Ephemeroptera and Trichoptera): the abundance of this group increased asymptotically as velocity increased. However, in that study, the modelled velocities were relatively low, and they do not disregard the fact that higher velocities might have changed the upper end of the curves, as high velocities are expected to decrease habitat suitability. In North America, Gore et al. (2001), it determined that the greatest diversity of aquatic macroinvertebrates was found at velocities between 0.6 m/s and 0.7 m/s. The increased abundance of other macroinvertebrates in this velocity range might also play a part in the presence of *Anacroneuria* and *Corydalus*, since both genera are predators (Contreras & Harris, 1998; Gutiérrez, 2010), however, it is clear that preference for higher velocity is not solely related to prey availability since many potential preys inhabit very low velocities. In our study, the maximum abundances of all four species of *Anacroneuria* were registered at slightly higher velocities (0.9 m/s).

With increasing velocity, an increment in viscosity also occurs (Dodds, 2002), which could make movement and displacement difficult for the organisms. This might be the reason why aquatic insects are less frequently found in extreme velocities. Gore et al. (2001) state that although these organisms have the necessary adaptations for living in sites with high velocities, they avoid environments where energy loss exceeds the gain. On the other hand, at low velocities (< 0.4 m/s) no *Anacroneuria* nymphs and only a few *Corydalus* larvae were collected. This is expected since these organisms depend on high concentrations of DO, and higher water velocities increase the concentration and renovation of DO (Genkai-Kato et al., 2005; Chapra et al., 2021), as also seen in this study, with a slight increase in the DO concentration with the velocity category.

Regarding neotropical rivers, similar velocity preferences were observed when the Threshold Indicator Taxa Analysis (TITAN) was used in two studies: Hanh et al. (2018) in Ecuador determined that the velocity threshold for Corydalidae was between 0.2 m/s and 1.0 m/s, while Perlidae had a lower current velocity threshold between 0.4-0.6 m/s. Quesada-Alvarado et al. (2020) in the Naranjo river watershed, Costa Rica, determined that the threshold for Corydalidae was between 0.3 m/s and 1.5 m/s, while Perlidae had a threshold between 0.5 m/s and 1.2 m/s.

Despite a preference for high velocities for the genus *Corydalus*, the bigger individuals (≥ 60 mm) were found in areas with low velocity (< 0.4 m/s), and even in waters with no current at all. This behavior can be explained since movement of bigger individuals is more restricted by density, viscosity and velocity of water (Sagnes et al., 2008), but most importantly, larvae from *Corydalus* pupate in terrestrial habitats, therefore, when they are ready to transition into adults, they approach the riverbanks (Cover & Resh, 2008). On the contrary, smaller larvae are found in areas with higher velocities and further away from the riverbanks, possibly to protect themselves from predators and to predate among other organisms, which are more abundant in higher velocity habitats. Hence, habitat selection of *Corydalus* depends on their larval stage, and we recommend separating *Corydalus* sizes for habitat modeling, similar to what is done with fish (*e.g.* Yao et al., 2018).

In general, larvae and nymphs from the two studied orders showed a higher dependency on velocity than water depth, since a wider habitat selection range was observed for depth. These results agree with those exposed by Waddle & Holmquist (2011), who affirm that larvae select their microhabitat as a function of velocity and substrate, and only up to some extent according to water depth. In our study, in the Savegre river, both *Anacroneuria* and *Corydalus* preferred water depths between 16 to 38 cm, similar to the results obtained by Gore et al. (2001) where larvae were most frequently found between depths of 20 to 25 cm. Furthermore, Shearer et al. (2015) recorded the greatest abundance of aquatic macroinvertebrates at depths less than 0.50 m, and Kim & Choi (2018) registered the same pattern where shallow depths were the most preferred. However, according to Alonso (2009), organisms can colonize at water depths of up to 1.5 m in areas of fast water current. This statement could not be confirmed in the present study, because for personal safety reasons, sampling in the Savegre river was not executed at depths greater than 1 m. Therefore, we cannot conclude about microhabitat preferences at such depths. This is why we decided to model the depth habitat preference using only the information provided by the panel of experts and the literature (Shearer et al., 2015, Kim & Choi, 2018).

We conclude that, due to their narrow range of optimal velocities and high ecological requirements, *Anacroneuria* larvae can be considered as an umbrella species if they are to be used in habitat availability modeling for flow studies. Eco-hydraulic models, in turn, are a tool that allows us to observe how changes in water volume can favor or reduce available habitat for aquatic insect larvae.

Eco-hydraulic models show one of the practical applications that can benefit from information on aquatic insect habitat preferences and flow variations. We demonstrate how watershed management can take advantage of field-specific biological data to technically support a regulatory decision, such as environmental flow. For example, in Costa Rica, legal regulations recommend the establishment of an environmental flow that represents 10 % of the mean annual flow. For the Savegre river this would represent ~ 8 m^3/s. However, with the preference information gathered by this study for *Anacroneuria* and *Corydalus*, and the habitat models created for site S1, we estimated that a flow of 13 m^3/s generates the greatest amount of optimal habitat for both larvae. Therefore, in the face of the possible use of the water resource, it is necessary to consider maintaining flows that provide the greatest amount of optimal habitat needed by the species that inhabit the rapids, since rapids and waterfalls are the first habitats to be damaged by a decrease in flow (Cortes et al., 2002).

This work contributes to expanding knowledge on aquatic insects' habitat preferences, which are typically scarce or nonexistent in tropical regions. Similarly, it is a valuable contribution to the field of ecohydraulics in the tropics, as most studies originate from temperate zones (Vázquez et al., 2020). Because *Anacroneuria* nymphs respond positively to increased water velocity and *Corydalus* larvae change their habitat preference according to their body size (with dependence on distance from the bank edge), it is necessary to take into account aquatic macroinvertebrates as bioindicators of flow to maintain ecosystem health, especially when there are changes in the hydraulic and hydrological regimes. The different assemblages of aquatic macroinvertebrates that use this type of habitat could be at risk when there are hydraulic changes. For future work on habitat preferences, methodologies that allow sampling of the rapid zones at greater depths (> 1m) should be implemented because in the rainy season the supply of depths and velocities of the river increases, and the insects may prefer or use greater depths. This would represent a change in the dynamics of preference which ecohydraulic models are ignoring. Finally, field studies on habitat preferences involving native organisms are highly recommended for modeling habitats in watershed management and environmental flow.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

See supplementary material
a65v73n1-suppl. 1

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REFERENCES

Alonso, P. (2009). *Estudio de macroinvertebrados bentónicos del sistema ambiental regional del proyecto de aprovechamiento hidráulico paso de la Reina, Oaxaca* [Manuscrito no publicado].

Angulo, A., Garita-Alvarado, C. A., Bussing, W. A., & López, M. I. (2013). Annotated checklist of the freshwater fishes of continental and insular Costa Rica: additions and nomenclatural revisions. *Check List*, *9*(5), 987–1019. http://dx.doi.org/10.15560/9.5.987

Balian, E. V., Segers, H. H., Lévêque, C., & Martens, K. (2008). The freshwater animal diversity assessment: an overview of the results. *Hydrobiologia*, *595*(1), 627–637. https://doi.org/10.1007/s10750-007-9246-3

Baptista, D. F., Buss, D. F., Dorvillé, L. F. M., & Nessimian, J. L. (2001). Diversity and habitat preference of aquatic insects along the longitudinal gradient of the Macaé River basin, Rio de Janeiro, Brazil. *Revista Brasileira de Biologia*, *61*(2), 249–258. https://doi.org/10.1590/S0034-71082001000200007

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *365*(1550), 2245–2254. https://doi.org/10.1098/rstb.2010.0083

Bonada, N., Prat, N., Resh, V. H., & Statzner, B. (2006). Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. *Annual Review of Entomology*, *51*(1), 495–523. http://dx.doi.org/10.1146/annurev.ento.51.110104.151124

Bravo, F., Romero, D., Gutiérrez-Fonseca, P. E., & Echeverría-Sáenz, S. (2019). The description of *Anacroneuria suerre* sp. nov. from Costa Rica (Plecoptera: Perlidae) and using nymphs in ecotoxicological studies. *Zootaxa*, *4608*(2), 357–364. http://dx.doi.org/10.11646/zootaxa.4608.2.9

Chapra, S. C., Camacho, L. A., & McBride, G. B. (2021). Impact of global warming on dissolved oxygen and BOD assimilative capacity of the world's rivers: modeling analysis. *Water*, *13*(17), 2408–2408. https://doi.org/10.3390/w13172408

Chavarría-Pizarro, L., Watson-Hernández, F., Quesada-Alvarado, F., Serrano-Núñez, V., Bustos-Vásquez, A. L., Fernández-Chévez, K., Chacón-Gutierrez, J., & Guzmán-Arias, I. (2024). Determination of environmental flow using a holistic methodology in three river paths in the Tempisque River Basin, Costa Rica. *Hydrology, 11*(10), 159. https://doi.org/10.3390/hydrology11100159

Chaves, A., Krasovskaia, I., & Gottschalk, L. (2006, November). Environmental demands for sustainable regulation schemes in the humid tropics: Climate variability and change—hydrological impacts [Conference session]. *Proceedings of the Fifth FRIEND World Conference held at Havana, Cuba.* IAHS Press.

Chaves, A., Pacheco, A., Krasovskaia, I., & Gottschalk, L. (2010). RANA-ICE, a methodology to estimate compensatory runoff in Costa Rica. *Hydrological Sciences Journal, 55*(1), 198–199.

Contreras, A., & Harris, S. (1998). The immature stages of *Platyneuromus* (Corydalidae), with a key to the genera of larva Megaloptera of Mexico. *Journal of the North American Benthological Society*, *17*(4), 489–517. http://dx.doi.org/10.2307/1468368

Cortes, R., Ferreira, M. T., Varandas-Oliveira, S., & Oliveira, D. (2002). Macroinvertebrate community structure in a regulated river segment with different flow conditions. *River Research and Applications*, *18*(4), 367–382. https://doi.org/10.1002/rra.679

Cover, M. R., & Resh, V. H. (2007). Global diversity of dobsonflies, fishflies, and alderflies (Megaloptera; Insecta) and spongillaflies, nevrorthids, and osmylids (Neuroptera; Insecta) in freshwater. In E.V. Balian, C. Lévêque, H. Segers, K. Martens (Eds.), *Freshwater Animal Diversity Assessment. Developments in Hydrobiology* (Vol. 198). Springer. https://doi.org/10.1007/978-1-4020-8259-7_42

Holdridge, L. R. (1964). *Life zone ecology.* Tropical Science Center.

Dijkstra, K. D. B., Monaghan, M. T., & Pauls, S. U. (2014). Freshwater biodiversity and aquatic insect diversification. *Annual Review of Entomology*, *59*, 143–163. https://doi.org/10.1146/annurev-ento-011613-161958

Dodds, W. K. (2002). *Freshwater Ecology. Concepts and environmental applications*. Academic Press.

Extence, C., Balbi, D., & Chadd, R. (1999). River flow indexing using British benthic macroinvertebrates: A framework for setting hydroecological objectives. *Regulated Rivers: Research & Management, 15*(6), 543–574. https://doi.org/10.1002/(SICI)1099-1646(199911/12)15:6<543::AID-RRR564>3.0.CO;2-W

Espinoza-Cisneros, E. (2021). Percepciones sobre calidad del agua fluvial en administradores de unidades productivas de la cuenca del río Savegre, Costa Rica. *Revista de Ciencias Ambientales*, *55*(2), 71–90. https://dx.doi.org/10.15359/rca.55-2.4

Genkai-Kato, M., Mitsuhashi, H., Kohmatsu, Y., Miyasaka, H., Nozaki, K., & Nakanishi, M. (2005). A seasonal change in the distribution of a stream-dwelling stonefly nymph reflects oxygen supply and water flow. *Ecological Research*, *20*(2), 223–226. https://doi.org/10.1007/s11284-004-0029-2

Gore, J., Layzer, J., & Mead, J. (2001). Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers Research & Management*, *17*(4–5), 527–542. https://doi.org/10.1002/rrr.650

Gutiérrez-Fonseca, P. E. (2010). Capítulo 6: Plecoptera. *Revista de Biología Tropical*, *58*(Supplement 4), S139–S148.

Gutiérrez-Fonseca, P. E., & Springer, M. (2011). Description of the final instar nymphs of seven species from *Anacroneuria* Klapálek (Plecoptera: Perlidae) in Costa Rica, and first record for an additional genus in Central America. *Zootaxa*, *2965*(1), 16–48. http://dx.doi.org/10.11646/zootaxa.2965.1.2

Gutiérrez-Fonseca, P. E., Alonso-Rodríguez, A. M., Cornejo, A., Bailey, A. C., Maes, J. M., & Ramírez, A. (2015). New records of *Anacroneuria* Klapálek, 1909 (Plecoptera: Perlidae) for Central America. *Zootaxa*, *3994*(3), 445–448. https://doi.org/10.11646/zootaxa.3994.3.9

Hanh, T., Eurie, M., Boets, P., Lock, K., Damanik, M., Suhareva, N., Everaert, G., Van der Heyden, C., Dominguez-Granada, L., Thi, T., & Goethals, P. (2018). Threshold responses of macroinvertebrate communities to stream velocity in relation to hydropower dam: A case study from the Guayas River Basin (Ecuador). *Water, 10*(9), 1195. https://doi.org/10.3390/w10091195

Hauer, R. F., & Resh, V. H. (2002). Macroinvertebrates. In R. F. Hauer, & G. A. Lamberti (Eds.), *Methods in stream ecology* (pp. 436–464). Elsevier.

Im, D., Kang, H., Kim, K. H., & Choi, S. U. (2011). Changes of river morphology and physical fish habitat following weir removal. *Ecological Engineering*, *37*(6), 883–892. https://doi.org/10.1016/j.ecoleng.2011.01.005

Im, D., Choi, S. U., & Choi, B. (2018). Physical habitat simulation for a fish community using the ANFIS method. *Ecological Informatics*, *43*, 73–83. http://dx.doi.org/10.1016/j.ecoinf.2017.09.001

Jackman, S. (2020). *pscl: Classes and methods for R developed in the Political Science Computational Laboratory* (Version 1.5.5) [Software]. Stanford University. https://CRAN.R-project.org/package=pscl

Krasovskaia, I., & Rodríguez, C. (Eds.). (2007). *Determinación de una metodología para establecer el caudal de compensación en los ríos de Costa Rica a partir de dos estudios de caso* [Informe final]. Instituto Costarricense de Electricidad.

Kelly, D., Hayes, J., Allen, C., West, D., & Hudson, H. (2015). Evaluating habitat suitability curves for predicting variation in macroinvertebrate biomass with weighted usable area in braided rivers in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *49*(3), 398–418. https://doi.org/10.1080/00288330.2015.1040424

Kim, S. K., & Choi, S. U. (2018). Prediction of suitable feeding habitat for fishes in a stream using physical habitat simulations. *Ecological Modelling, 385*, 65–77. https://doi.org/10.1016/j.ecolmodel.2018.07.014

Laporte, S., Pacheco, A., & Rodríguez, C. R. (2006, November). Estimation of minimum acceptable (compensatory) flow for the rivers of Costa Rica. *Climate Variability and Change—Hydrological Impacts [Conference session]. Proceedings of the Fifth FRIEND World Conference held at Havana, Cuba.* IAHS Press.

Leopold, L. B., Wolman, M. G., & Miller, J. P. (1992). *Fluvial processes in geomorphology.* Dover Publications.

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 73: e2025450, enero-diciembre 2025 (Publicado Nov. 03, 2025)

Luiza-Andrade, A., Silva, R. R., Shimano, Y., Faria, J., Cardoso, M. N., Brasil, L. S., Ligeiro, R., Martins, R. T., Hamada, N., & Juen, L. (2022). Niche breadth and habitat preference of Ephemeroptera, Plecoptera, and Trichoptera (Insecta) in streams in the Brazilian Amazon. *Hydrobiologia, 849*, 4287–4306. https://doi.org/10.1007/s10750-022-04987-6

Noack, M., Schneider, M., & Wieprecht, S. (2013). The habitat modelling system CASiMiR: A multivariate fuzzy approach and its applications. In I. Maddock, A. Harby, P. Kemp, & P. Wood (Eds.), *Ecohydraulics: An integrated approach* (pp. 75–91). John Wiley & Sons.

Oksanen, J., Guillaume-Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan: Community ecology package* (Version 2.5-7) [Software]. https://CRAN.R-project.org/package=vegan

Quesada-Alvarado, F., Umaña, G., Springer, M., & Picado-Barboza J. (2020). Variación estacional y características fisicoquímicas e hidrológicas que influyen en los macroinvertebrados acuáticos, en un río tropical. *Revista de Biología Tropical*, *68*(Suplemento 2), S54–S67. https://doi.org/10.15517/rbt.v68iS2.44332

Quesada-Alvarado, F., Umaña, G., Springer, M., & Picado-Barboza, J. (2021). Classification of aquatic macroinvertebrates in flow categories for the adjustment of the LIFE Index to Costa Rican rivers. *Ecohydrology & Hydrobiology*, *21*(2), 368–376. https://doi.org/10.1016/j.ecohyd.2020.08.005

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rico, A., & Van, P. J. (2015). Evaluating aquatic invertebrate vulnerability to insecticides based on intrinsic sensitivity, biological traits, and toxic mode of action. *Environmental Toxicology and Chemistry*, *34*(8), 1907–1917. https://doi.org/10.1002/etc.3008

Rivera-Gasperín, S., Ardila-Camacho, A., & Contreras-Ramos, A. (2019). Bionomics and ecological services of Megaloptera Larvae (Dobsonflies, Fishflies, Alderflies). *Insects*, *10*(4), 86–86. https://doi.org/10.3390/insects10040086

Sagnes, P., Mérigoux, S., & Péru, N. (2008). Hydraulic habitat use with respect to body size of aquatic insect larvae: case of six species from a French Mediterranean type stream. *Limnologica*, *38*(1), 23–33. https://doi.org/10.1016/j.limno.2007.09.002

Shearer, K. A., Hayes, J. W., Jowett, I. G., & Olsen, D. A. (2015). Habitat suitability curves for benthic macroinvertebrates from a small New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, *49*(2), 1–14. http://dx.doi.org/10.1080/00288330.2014.988632

Starr, S. M., & Wallace, J. R. (2021). Ecology and biology of aquatic insects. *Insects*, *12*(1), 51. https://doi.org/10.3390/insects12010051

Stark, B. P. (2014). Records of Mesoamerican Anacroneuria (Plecoptera: Perlidae), with descriptions of four new species. *Illiesia*, *10*(02), 6–16. https://doi.org/10.5281/zenodo.4760479

Sumudumali, R. G. I., & Jayawardana, J. M. C. K. (2021). A review of biological monitoring of aquatic ecosystems approaches: with special reference to macroinvertebrates and pesticide pollution. *Environmental Management*, *67*, 263–276. https://doi.org/10.1007/s00267-020-01423-0

Tamaris-Turizo, C., Turizo-Correa, R. R., & Zúñiga, M. (2007). Distribución espacio-temporal y hábitos alimentarios de ninfas de Anacroneuria (Insecta: Plecoptera) en el río Gaira (Sierra de Nevada de Santa Marta, Colombia). *Caldasia*, *29*(2), 375–385.

Theodoropoulos, C., Papadonikolaki, G., Stamou, A., Bui, M. D., Rutschmann, P., & Skoulikidis, N. (2015, September 3–5). A methodology for the determination of environmental flow releases from dams based on hydrodynamic habitat modelling and benthic macroinvertebrates. In *Proceedings of the 14th International Conference on Environmental Science and Technology*. Rhodes, Greece.

Theodoropoulos, C., Vourka, A., Skoulikidis, N., Rutschmann, P., & Stamou, A. (2018). Evaluating the performance of habitat models for predicting the environmental flow requirements of benthic macroinvertebrates flow requirements of benthic macroinvertebrates. *Journal of Ecohydraulics*, *3*(1), 30–44. http://dx.doi.org/10.1080/24705357.2018.1440360

The United Nations Educational, Scientific and Cultural Organization. (2017). *Caja de herramientas para la determinación de caudal ambiental*. UNESCO

Vázquez, R. F., Vimos-Lojano, D., & Hampel, H. (2020). Habitat suitability curves for freshwater macroinvertebrates of tropical andean rivers. *Water*, *12*(10), 2703–2703. https://doi.org/10.3390/w12102703

Waddle, T. J., & Holmquist, J. G. (2011). Macroinvertebrate response to flow changes in a subalpine stream: predictions from two-dimensional hydrodynamic models. *River Research Appli*cations, *29*(3), 366–379.

Wood, S. N. (2017). *Generalized additive models: An Introduction with R (2nd ed.)* (Version 1.8-42) [Software]. https://CRAN.R-project.org/package=mgcv

Yao, W., Bui, M. D., & Rutschmann, P. (2018). Development of eco-hydraulic model for assessing fish habitat and population status in freshwater ecosystems. *Ecohydrology*, *11*(5), e1961. https://doi.org/10.1002/eco.1961