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Ecological relevance of non-perennial rivers for the conservation of terrestrial and aquatic communities

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Abstract

River conservation efforts traditionally focus on perennial watercourses (i.e., those that do not dry) and their associated aquatic biodiversity. However, most of the global river network is not perennial and thus supports both aquatic and terrestrial biodiversity. We assessed the conservation value of nonperennial rivers and streams (NPRS) in one of Europe's driest regions based on aquatic (macroinvertebrates, diatoms) and terrestrial (riparian plants, birds, and carabid beetles) community data. We mapped the distribution of taxa at 90 locations and across wide environmental gradients. Using the systematic planning tool Marxan, we identified priority conservation sites under 2 scenarios: aquatic taxa alone or aquatic and terrestrial taxa together. We explored how environmental factors (runoff, flow intermittence, elevation, salinity, anthropogenic impact) influenced Marxan's site selection frequency. The NPRS were selected more frequently (over 13% on average) than perennial rivers when both aquatic and terrestrial taxa were considered, suggesting that NPRS have a high conservation value at the catchment scale. We detected an underrepresentation of terrestrial taxa (8.4–10.6% terrestrial vs. 0.5–1.1% aquatic taxa were unrepresented in most Marxan solutions) when priority sites were identified based exclusively on aquatic biodiversity, which points to a low surrogacy value of aquatic taxa for terrestrial taxa. Runoff explained site selection when focusing on aquatic taxa (all best-fitting models included runoff, $r^2 = 0.26$–0.27), whereas elevation, salinity, and flow intermittence were more important when considering both groups. In both cases, site selection frequency declined as anthropogenic impact increased. Our results highlight the need to integrate terrestrial and aquatic communities when identifying priority areas for conservation in catchments with NPRS. This is key to overcoming drawbacks of traditional assessments based only on aquatic taxa and to ensure the conservation of NPRS, especially as NPRS become more prevalent worldwide due to climate change and increasing water demands.

KEYWORDS
aquatic macroinvertebrates, birds, carabid beetles, diatoms, intermittent rivers, Marxan, Mediterranean rivers, non-perennial rivers, riparian vegetation

Resumen

Los esfuerzos de conservación fluvial se enfocan tradicionalmente en los cauces permanentes (aquellos que no se secan) y la biodiversidad acuática asociada. Sin embargo, la mayor parte de la red hidrográfica mundial no es permanente, por lo que sustenta biodi-

versidad tanto acuática como terrestre. Evaluamos el valor de conservación de los ríos y arroyos no permanentes (RANP) en una de las regiones más secas de Europa con datos de comunidades acuáticas (macroinvertebrados, diatomeas) y terrestres (escarabajos carábidos). Mapeamos la distribución de los taxones en 90 localidades que cubren gradientes ambientales amplios. Con la herramienta de planificación sistemática Marxan identificamos los sitios prioritarios de conservación bajo dos escenarios: considerando sólo los taxones acuáticos o los taxones acuáticos y terrestres juntos. Exploramos cómo los factores ambientales (escorrentía, intermitencia del caudal, altitud, salinidad, impacto antropogénico) influyeron sobre la frecuencia de selección de sitio de Marxan. Los RANP fueron seleccionados con mayor frecuencia (más del 13% en promedio) que los ríos permanentes cuando consideramos los taxones acuáticos y terrestres, lo que sugiere que los RANP tienen un valor elevado de conservación a escala de cuenca. Detectamos que los taxones terrestres estaban infrarrepresentados (8.4-10.6% taxones terrestres vs. 0.5-1.1% acuáticos no tuvieron representación en la mayoría de las soluciones de Marxan) cuando los sitios prioritarios para la conservación se identificaban exclusivamente con la biodiversidad acuática, lo que indica que los taxones acuáticos tienen un reducido valor indicador para los taxones terrestres. La escorrentía determinó la selección de sitios cuando se basó en los taxones acuáticos (los mejores modelos incluyeron la escorrentía, $r^2 = 0.26$-0.27), mientras que la altitud, la salinidad y la intermitencia del caudal fueron más importantes cuando se consideraron ambos grupos. En ambos casos, la frecuencia de selección disminuyó conforme se incrementó el impacto antropogénico. Nuestros resultados resaltan la necesidad de integrar las comunidades terrestres y acuáticas a la identificación de las áreas prioritarias para la conservación de la biodiversidad en cuencas con RANP. Lo anterior es importante para superar las evaluaciones tradicionales basadas solamente en los taxones acuáticos y para garantizar la conservación de los RANP, especialmente ahora que estos son cada vez más frecuentes a nivel mundial debido al cambio climático y a la creciente demanda de agua.

PALABRAS CLAVE
aves, diatomeas, escarabajos carábidos, macroinvertebrados acuáticos, Marxan, ríos intermitentes, ríos mediterráneos, ríos no permanentes, vegetación ribereña

INTRODUCTION

Biodiversity loss is great worldwide but is especially accentuated in freshwater ecosystems, which harbor a disproportionately large fraction of the world's total biodiversity relative to their extent (Reid et al., 2019). Freshwater biodiversity loss and the decline in ecosystem services reflect the poor conservation status of these ecosystems due to global change (Tickner et al., 2020; van Vliet et al., 2017). Thus, effective and systematic approaches are urgently needed to address potential trade-offs between multiple objectives in these ecosystems (e.g., energy production and biodiversity conservation [Hermoso et al., 2018]).

In freshwater ecosystems, nonperennial rivers and streams (NPRS)—those that experience recurrent drying—constitute over half the length of the global river network and are increasing in extent globally due to climate change, land-use intensification, and water abstraction (Messager et al., 2021; Tramblay et al., 2021). However, current paradigms in river science and conservation have emerged from and been developed for perennial rivers (Allen et al., 2020). For example, in Europe the Water Framework Directive excludes NPRS almost entirely from its ecological status assessment and recovery goals (Munné

et al., 2021) because they do not meet the criteria established for the definition of water bodies (WFD 2000/60/EC) (Skoulikidis et al., 2017). Also, NPRS are underrepresented in the most important conservation frameworks (Fritz et al., 2017), such as the RAMSAR Convention (1971) and the Habitats Directive (92/43/CEE). This poor representation is particularly problematic in semiarid regions, where agricultural intensification and climate change are causing widespread degradation of NPRS (Chiu et al., 2017). Besides land-use pressures and associated alteration of natural flow regimes, natural stressors (e.g., salinity, altitude) could also modulate the contribution of NPRS to river biodiversity at the catchment scale (Suárez et al., 2017).

NPRS have a high conservation value because their hydrological and habitat conditions vary considerably over time, which allows the sequential occurrence of different aquatic and terrestrial communities (i.e., temporal turnover [Bogan & Lytle, 2007; Stubbington et al., 2017]); they contain rare and endemic habitat specialists adapted to strong seasonal abiotic filtering (e.g., desiccation, osmotic pressure, low oxygen [Bunting et al., 2021; Datry et al., 2017; Millán et al., 2011]); and they provide high-quality habitat for terrestrial species during the dry phase (Sánchez-Montoya et al., 2017, 2020, 2022; Steward et al., 2022). Moreover, due to their recurrent transitions between aquatic

and terrestrial habitats (wet–dry phases), NPRS offer a prime opportunity to explore how integrated planning across ecosystem boundaries can improve the conservation of both terrestrial and aquatic biodiversity (Giakoumi et al., 2019; Hermoso et al., 2021). For example, Leal et al. (2020) reported more than 1500 terrestrial and freshwater species in the Amazon and found that integrated cross-realm planning increases freshwater benefits by up to 600%. This is important because terrestrial and freshwater ecosystems are tightly linked through many different processes, such as energetic regulation and exchange (Richardson & Sato, 2015) and trophic interactions (Knight et al., 2005). Cross-boundary research has thus been advocated in these systems (Erős & Campbell Grant, 2015; Soininen et al., 2015).

Using data from a semiarid Mediterranean catchment, we assessed the conservation value of NPRS for aquatic and terrestrial biodiversity and how this value could complement that of perennial rivers and streams (PRS). To do this, we gathered occurrences of aquatic (macroinvertebrates and diatoms) and terrestrial (riparian vegetation, birds, and carabid beetles) biological communities and used the systematic planning software Marxan to identify priority sites for biodiversity conservation. More specifically, we assessed the conservation value of NPRS, as represented by both aquatic and terrestrial taxa, relative to PRS; evaluated the potential of aquatic biodiversity to serve as surrogates of terrestrial organisms associated with watercourses and riparian habitats; and identified the environmental factors influencing the selection of priority sites for conservation by Marxan, with the aim of representing aquatic taxa only or both terrestrial and aquatic taxa. We expected that NPRS would be more frequently selected than PRS to represent both aquatic and terrestrial taxa; aquatic taxa would not be good surrogates of terrestrial taxa due to their differential dependence on aquatic habitats; and site selection frequency by Marxan would be determined by a combination of anthropogenic impacts, habitat characteristics, and catchment-scale environmental gradients.

METHODS

Study area

The Segura River basin is a Mediterranean catchment in one of the most arid zones in Europe (Figure 1). Despite its relatively small size (18,870 km^2), it covers wide anthropogenic (organic enrichment, water abstraction, and physical channel alteration) and natural (climatic, altitudinal, and lithological) environmental gradients (Mellado-Díaz et al., 2008). Its geology ranges from calcareous rocks, such as dolomite and limestone with varied karstic relief in headwaters, to limestone and salt-rich tertiary marls in middle reaches and lowlands. Average yearly precipitation is 362 mm (historical series: 1980/1981−2005/2006; https://www.chsegura.es), but climate ranges from subhumid in the northwestern mountains to semiarid in the southeastern lowlands. This results in a hydrological gradient of increasing flow variability from PRS (i.e., sites with no days with flow <0.001 m^3/s) to NPRS (≥1 day per year with no flow according to the SIMPA model [see "Effects of environmental predictors
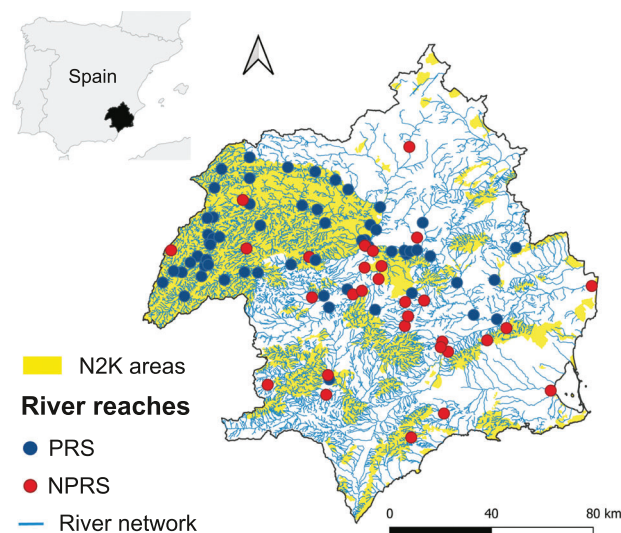
FIGURE 1 Location of Segura River catchment and the studied perennial rivers and streams (PRS) and nonperennial rivers and streams (NPRS) (N2K, Natura 2000 area)

on site selection frequency" section]) in the study area (Belmar et al., 2011). The river network ranges from sparsely populated forested headwaters, where most protected areas are located, to densely populated lowland cities and agricultural areas with a predominantly shrubby landscape. Agriculture constitutes the main land use (>50% estimated from CORINE Land Cover 2018), and associated irrigation causes seasonal reductions in stream flows. Although the protected area network supports a relatively high number of species of conservation concern, the distribution and extent of reserves is still insufficient to protect freshwater biodiversity (Abellán et al., 2007), particularly in NPRS (Gómez et al., 2005).

Biodiversity data

We selected 5 biological groups that represent aquatic (macroinvertebrates and diatoms) and terrestrial (vegetation, birds, and carabid beetles in riparian zone) communities responsive to environmental variability and for which occurrence data were available from environmental agencies and taxonomic experts. Some of these taxonomic groups contain species that range from strictly aquatic organisms to terrestrial organisms. Organisms in these groups sustain a wide range of ecosystem functions. Therefore, changes in the communities of these 5 groups can influence trophic interactions, organic matter production and processing, nutrient cycling, aquatic and riparian microclimates, bank stability, and water quality and availability (Riis et al., 2020; Sánchez-Montoya et al., 2017; Stubbington et al., 2018, 2019, 2020). We compiled information from 162 sites (83 PRS and 79 NPRS) covering the main natural and anthropogenic gradients in the study area. A different number of sites was available for each studied group (Appendix S1).

Diatom species records were compiled from databases of the Segura Water Agency for 61 sites surveyed once between

April and June from 2008 to 2010. Diatoms were originally sampled following the water quality protocol of the guidance standard (EN 13946:2003) for routine sampling and pretreatment of benthic diatoms from rivers (CEN, 2003) and the Ebro Hydrographic Confederation protocol for sampling, identification, and sorting (Cambra et al., 2005). The protocol consisted mainly of scraping or brushing of 5–10 submerged cobbles, small boulders, or macrophytes (if cobbles and boulders were absent) with a total sampling surface area of approximately 100 cm^2 in river reaches 10 m long and a subsequent lab procedure of preservation, cleaning, preparation of permanent slides, and microscopic identification.

Aquatic macroinvertebrates were sampled from 77 sites once from May to August in 2010–2012. We used a multihabitat sampling protocol (500-μm kick net) in which sampling effort was proportional to the occurrence of each habitat (Jáimez-Cuéllar et al., 2002). In the laboratory, Ephemeroptera, Trichoptera, Plecoptera, Odonata, Coleoptera, and Hemiptera were identified to genus and species when possible, whereas the remaining taxa (Diptera and non-insect taxa) were identified to family.

Riparian vegetation was surveyed at 81 sites once from May to August in 2010–2012 along 500-m reaches on both river margins, where we noted the occurrence of perennial species along 10 transects, thus obtaining a list of native species (few taxa identified to genus level) for each site (Bruno et al., 2014; Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, et al., 2016).

Birds were surveyed at 43 sites once from April to June in 2000–2017. These records were compiled from an academic (E065-03 ECOMED Research Group, University of Murcia) and a citizen science (ebird.org) database. Species data were collected through visual or audio contacts by skilled birdwatchers in the riparian zone. All species linked to riparian habitats were considered, including obligate riparian birds (Rich, 2002) and riparian-dependent and facultative species (forest and aquatic species seeking refuge in riparian vegetation and aerial feeders foraging in the riparian interface).

We compiled carabid species records from 54 riparian zones from 2 databases (Andújar et al., 2000; Ortiz et al., 1987) and unpublished data (expert J.L. Lencina). The data were namely collected from April to August in 1998–2018. Depending on species' habitat and vegetation density, carabids were collected using different methods, such as pitfall traps (remaining 5 months in dense riparian forests), light traps (over 1 night), hand nets (flyers), and quadrat sampling by hand and aspirator (small species). This integrative approach is considered appropriate to reach a complete qualitative characterization of carabid diversity (Ortiz et al., 1987).

For each taxonomic group, our data set included 1 sample per site collected during low-flow conditions (late spring and early summer). Carabid and bird data were collected over a greater sampling period than aquatic macroinvertebrates, diatoms, and vegetation. Except for riparian vegetation, terrestrial groups have been traditionally ignored when monitoring and assessing riverine biodiversity in the study area, so a broader time span was necessary to reach representative data sets. From the compiled data, we selected only those sites that contained records of at least 1 group of both aquatic and terrestrial taxa. Accordingly,

90 sites (60 PRS and 30 NPRS; 50 with information for diatoms, 78 for aquatic macroinvertebrates, 81 for riparian vegetation, 25 for birds, and 24 for carabid beetles) covering the main natural and anthropogenic gradients were selected for Marxan analysis (Figure 1; Appendix S1).

Identification of priority sites for conservation

We used Marxan, a commonly used spatial conservation prioritization tool (Ball et al., 2009), to evaluate the conservation value of the PRS and NPRS in the selected sites (90; 60 PRS and 30 NPRS) under 2 alternative scenarios: considering only aquatic taxa (hereafter, only-aquatic scenario) or aquatic and terrestrial taxa simultaneously (hereafter, all-taxa scenario). Marxan tries to minimize an objective function composed of 2 main parameters (Equation 1): cost, which represents the sum of the individual costs of all sites selected as part of the solution, and feature penalties, which are applied when the targets set are not fully achieved. In our case, the targets were the total number of occurrences of each taxon. The feature penalty is also weighted by a taxon penalty factor (SPF), which multiplies the individual taxon penalties and indicates the relative importance of achieving targets for each taxon individually. Large SPF weights force Marxan to achieve the targets regardless of the cost. We set a high SPF value for all taxa (SPF = 10) to ensure full achievement of targets across scenarios and did not include connectivity constraints. Marxan applies the following mathematical function:

$$\text{Objective function} = \sum_{i=1}^{m} c_i\, x_i + \sum_{j=1}^{n} \text{SPF}_j\, \text{FR}_j\, H\,(s) \left(\frac{s}{t_j} \right),$$

(1)

where x_i is a control variable that takes a value of 1 when the planning unit i is selected and 0 otherwise; i belongs to the group of m planning units; c_i is the cost of planning unit i; SPFj is a taxon penalty factor that applies when the desired representation target for each taxon j is not achieved; $H(s)$ is a Heaviside function that takes a value of 0 when $s/t_j \le 0$ and 1 otherwise; s is the shortfall in targets not achieved and is measured as $t_j -$ representation achieved; $s/t_j = 1$ when taxon j is not represented in the solution and approaches 0 as the level of representation approaches the target amount (t_j).

Given the high rate of taxa turnover in our data set, with most taxa restricted to 1 or a few sites, high representation targets could only be achieved for all taxa at the same time by selecting almost all sites simultaneously. To address this problem, we set a low requirement for the number of occurrences that each taxon needed to be selected (target = 1) and carried out 3 bootstrap levels analyses for each scenario by attempting to cover the distribution of a given proportion of all taxa (50%, 75%, and 90%). For this, we selected 1000 random samples from the pool of taxa under each scenario and identified the minimum set of locations to cover at least 1 occurrence for each of these taxa. Given the lack of estimates of conservation costs across the study area, we used a constant cost across all locations (e.g., Hermoso et al., 2021). With this configuration, we ran Marxan

100 times, with 1.5 million iterations per run, and kept the solution with the lowest objective function score across those runs as our best solution for each of the bootstrap selection of taxa. We then summarized all best solutions by calculating the selection frequency of each location across the 1000 solutions for each bootstrap level and scenario individually. We therefore had 6 different selection-frequency values for each location: 3 bootstrap levels (50%, 75%, and 90%) in 2 scenarios (only aquatic or all taxa).

Representation of aquatic and terrestrial biodiversity in Marxan solutions

To explore the surrogacy value of aquatic taxa for terrestrial taxa, we calculated the mean representation (mean number of occurrences) of each aquatic and terrestrial taxon and the number of times that each taxon did not achieve its representation target in solutions obtained under the only-aquatic scenario in comparison with the all-taxa scenario. For the latter, we also quantified the number of times a taxon was not included both in at least 1 solution and half of the solutions out of the 1000 bootstraps. We used Mann–Whitney–Wilcoxon tests to determine the significance of differences. We expected to find significant differences in the representation of aquatic and terrestrial taxa in solutions when we used only aquatic taxa and a different incidence of targets not achieved across aquatic and terrestrial taxa. This would reveal a low capacity of aquatic taxa to act as surrogates for terrestrial groups and would not support current river conservation strategies focusing mainly on aquatic taxa conservation.

Effects of environmental predictors on site selection frequency

We estimated 5 environmental predictor variables at each site to represent hydrological, climatic, lithological, topographical, and anthropogenic gradients in the study area: mean annual runoff (hereafter, runoff [mm]), flow intermittence (mean number of dry- and no-flow days per year), elevation (meters above sea level), salinity, and anthropogenic impact (see Appendix S1 for detailed distribution and values). Runoff and flow intermittence were derived from the rainfall–runoff simulation model SIMPA (Estrela & Quintas, 1996) based on 25 years (1980/1981–2005/2006) of daily discharge data. Elevation was derived from a 25-m digital elevation model. Principal component analysis (PCA) was performed on water electrical conductivity, rock conductivity and hardness, terrain permeability, and calcareous and sedimentary rocks in and upstream of the river reach to characterize the salinity gradient. Salinity was represented in the subsequent analysis by the first axis, which explained 39% of total variance. Water conductivity was measured in situ, and all other variables were calculated from maps (1:50,000) provided by the Geological and Mining Institute of Spain-IGME. Anthropogenic impacts were estimated as the inverse value of the Mediterranean reference criteria from Sánchez-Montoya

et al. (2009). This represents human impact levels based on 20 equally weighted criteria that relate to the riparian zone, invasive species, point and diffuse sources of pollution, land use, river morphology and instream habitat characteristics, hydrological conditions, and flow regulation.

Mann–Whitney–Wilcoxon tests were performed to compare NPRS and PRS selection frequencies under the 2 scenarios and the 3 bootstrap levels (50%, 75%, and 90%). Then, we used multiple regression models and hierarchical variance partitioning to explore patterns of site selection frequency along continuous environmental gradients (Walsh & Mac Nally, 2008). To evaluate their relative importance, we grouped environmental predictors into hydrological (runoff and flow intermittence) and non-hydrological (elevation, anthropogenic impacts, and salinity) variables. Models were ranked based on Akaike information criteria corrected for small sample sizes (AICc); the top-ranked model had the lowest AICc. To linearize sigmoid distributions of site selection frequency, we applied a logit transformation. Prior to analysis, to reduce skewness, runoff and salinity were log transformed and elevation, anthropogenic impact, and flow intermittence were square-root transformed when necessary. Environmental predictors were Z standardized (mean [SD] = 0 [1]) to allow for model coefficient comparison. The variance inflation factor (VIF) was calculated to check predictor collinearity (Zuur et al., 2010). When high collinearity between 2 predictors was found in a group, alternative models for nonredundant predictors were used to avoid highly correlated variables (VIF > 2, pairwise Pearson's $r > 0.7$) within the same group of predictors. Spatial autocorrelation of the model residuals was checked using Moran's tests. We visually checked the normality and homoscedasticity of model residuals (Zuur et al., 2010).

RESULTS

A total of 899 taxa were recorded in the 90 study sites: 472 aquatic (230 macroinvertebrates and 242 diatoms) and 427 terrestrial (228 native riparian plants, 86 birds, and 113 carabid beetles) (Appendix S2). As expected, the number of sites required to achieve the representation target increased as the number of taxa to be represented increased (bootstrap levels 50%, 75%, and 90%). As more taxa were represented and sites included, we observed a greater average selection frequency and less variability in the combination of sites suitable to represent target taxa. Accordingly, the all-taxa scenario consistently showed higher average site selection frequency than the only-aquatic scenario (Figure 2).

Representation of aquatic and terrestrial biodiversity in Marxan solutions

The mean number of occurrences of aquatic and terrestrial taxa was consistently greater in the all-taxa scenario relative to the only-aquatic one. This pattern was consistent across all bootstrap levels, especially for terrestrial taxa. When all taxa were
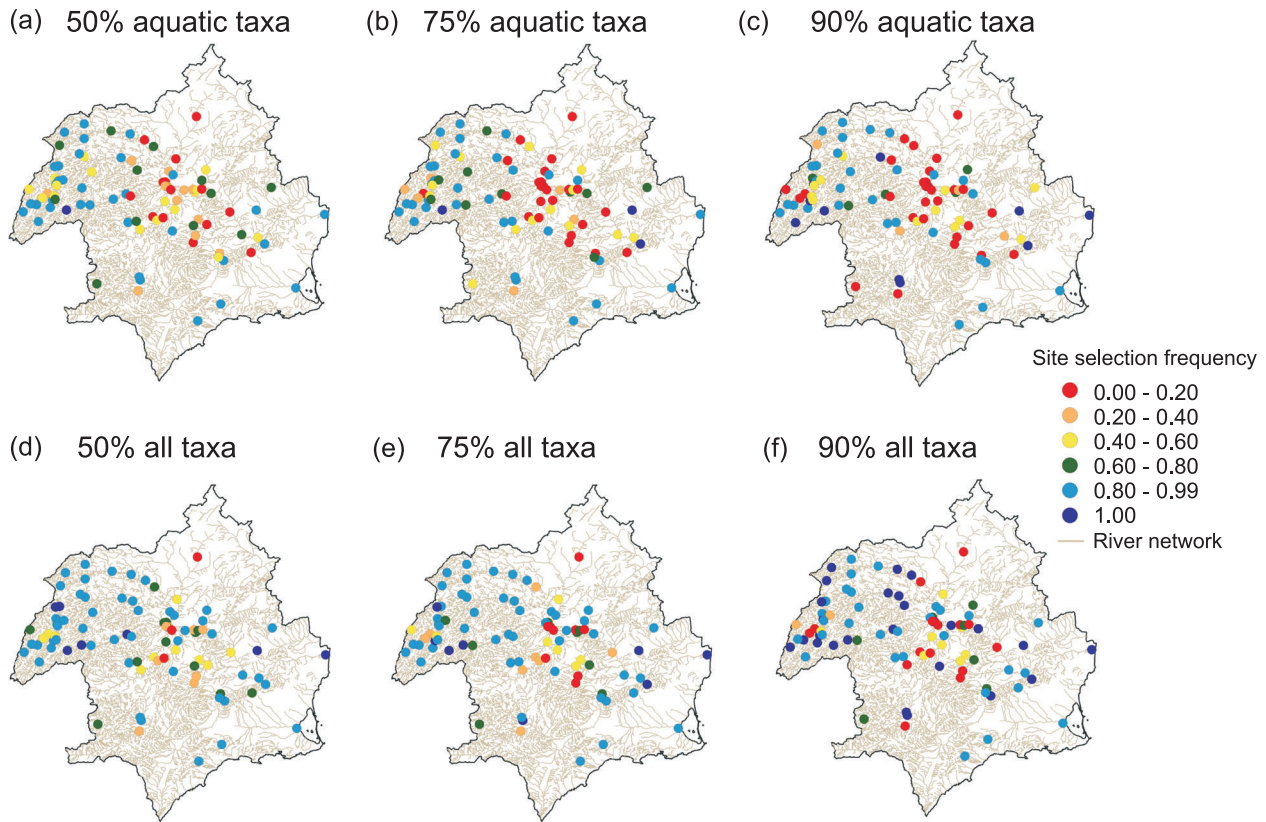
FIGURE 2 Distribution of Marxan site selection frequencies across the study area when using (a, b, c) only aquatic taxa and (d, e, f) aquatic and terrestrial taxa at 3 thresholds of taxa representation (50%, 75%, and 90%)

TABLE 1 Mean number of occurrences of taxa in Marxan solutions (SE 0.2–0.3) and number of taxa that did not achieve the representation target in at least 1 and 500 of Marxan solutions (out of 1000 bootstraps) when using only aquatic (Aq) and when using aquatic and terrestrial (All) taxa for Marxan site selection at 3 thresholds of taxa representation (50%, 75%, and 90%)

	50% of taxa		75% of taxa		90% of taxa	
	Aq taxa	All taxa	Aq taxa	All taxa	Aq taxa	All taxa
Mean taxa occurrences	4.3	5.4	4.2	5.3	4.1	5.2
Mean terrestrial taxa occurrences	3.5	4.8	3.4	4.7	3.3	4.6
Mean aquatic taxa occurrences	5.1	6.1	5	5.9	4.8	5.8
Unrepresented taxa (%) in ≥1 solution	51.9	25.4	43.9	21.3	36.1	11.3
Unrepresented terrestrial taxa (%) in ≥1 solution	63.2	24.2	57.8	22.1	51.5	11.3
Unrepresented aquatic taxa (%) in ≥1 solution	41	26.5	30.5	20.6	21.2	11.3
Unrepresented taxa (%) in ≥500 solutions	4.7	0.3	5.2	0.4	6.0	0.4
Unrepresented terrestrial taxa (%) in ≥500 solutions	8.4	0.2	9.5	0.2	10.6	0.4
Unrepresented aquatic taxa (%) in ≥500 solutions	1.1	0.5	1.1	0.7	1.6	0.5

considered, the mean number of aquatic taxa occurrences in Marxan solutions was significantly higher than that of terrestrial occurrences (Mann–Whitney–Wilcoxon test; $p = 0.01-0.02$) (Table 1). These differences were much more evident in the only-aquatic scenario ($p < 0.001$ for all bootstrap levels [i.e., 50%, 75%, and 90%]) (Appendix S3).

The proportion of taxa that did not achieve their representation targets in at least 1 solution or ≥50% of the 1000 bootstrap solutions was higher under the only-aquatic scenario than in the all-taxa scenario and was highest for terrestrial taxa under the only-aquatic scenario. In fact, the first 27 (50% threshold), 32 (75%), and 41 (90%) most frequently underrepresented taxa
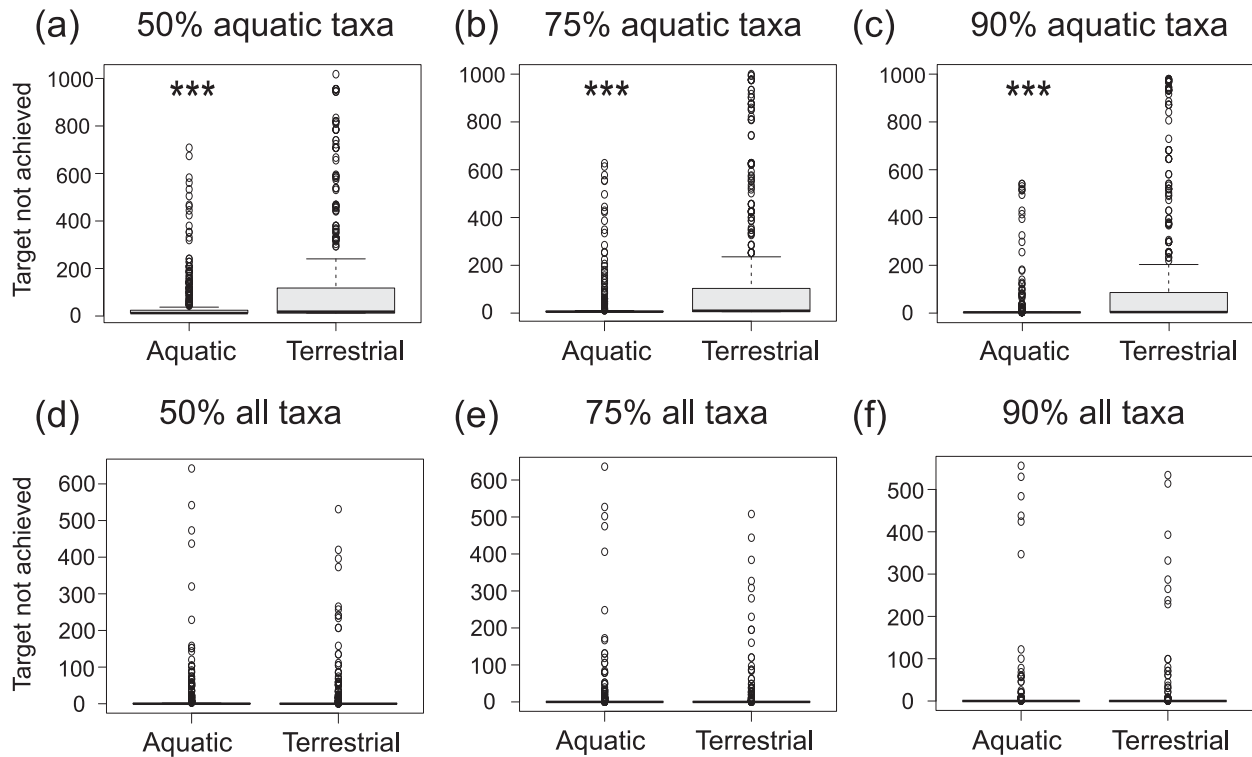
FIGURE 3 Number of times that aquatic and terrestrial taxa were not represented (i.e., times target was not achieved) (Mann–Whitney–Wilcoxon test ***$p < 0.001$) when using (a, b, c) only aquatic and (d, e, f) aquatic and terrestrial taxa at 3 thresholds of taxa representation (50%, 75%, and 90%) in Marxan prioritization analyses (horizontal line, median; box ends, interquartile range; whiskers, observed maxima and minima; points, outliers)

in this scenario were terrestrial. These differences were even greater for the number of taxa that did not achieve their representation target in ≥50% of the solutions (Table 1). Accordingly, terrestrial taxa tended to miss their representation targets more often than aquatic taxa in the only-aquatic scenario across the 3 bootstrap levels (Mann–Whitney–Wilcoxon test, $p < 0.001$) (Figure 3), indicating that aquatic taxa were a poor surrogate for terrestrial taxa. Representation of aquatic and terrestrial taxa was comparable in the all-taxa scenario ($p = 0.6–1.0$, depending on the conservation threshold); only 3–4 taxa remained substantially unrepresented (i.e., excluded from >50% of the solutions).

Relationships between environmental variables and site selection frequency

In the only-aquatic scenario, both hydrological (runoff) and non-hydrological (elevation, anthropogenic impacts) variables were included in the best-fitting models that explained site selection frequency. In the all-taxa scenario, these best-fitting models included only non-hydrological variables (elevation, anthropogenic impacts, and salinity). These patterns were consistent across all bootstrap levels considered for only-aquatic ($r^2 = 0.26–0.27$) and all-taxa ($r^2 = 0.20–0.28$) (Table 2) scenarios. Non-hydrological variables, such as elevation and

anthropogenic impacts, were included in all best-fitting models that explained site selection frequency (all the variable combinations tested are in Appendix S3).

A significant convex quadratic relationship was found between elevation and site selection frequency. This relationship was relatively consistent across bootstrap levels and both scenarios ($p < 0.01$ in all cases), but it was much stronger in the only-aquatic scenario (Figure 4). Selection frequency decreased as anthropogenic impact decreased for both only-aquatic and all-taxa scenarios (Figure 4). The sites selected most frequently to represent aquatic communities were also those with higher runoff, whereas sites with intermediate runoff were chosen least frequently (i.e., convex quadratic response). The frequency of site selection decreased as salinity increased, especially when all taxa were included, but salinity was also significant in the second-best models of the only-aquatic scenario) (ΔAIC < 4).

Although flow intermittence was not included in any top models, it was included in the second-best model (ΔAIC < 4) for all the bootstrap levels in the all-taxa scenario (Appendix S3). Accordingly, NPRS were selected more frequently than PRS to represent 50% (Mann–Whitney–Wilcoxon test, $p = 0.011$), 75% ($p = 0.004$), and 90% ($p = 0.008$) of all taxa (Figure 5). In contrast, when considering aquatic taxa exclusively, we observed comparable selection frequencies of PRS and NPRS (Mann–Whitney–Wilcoxon test, $p = 0.2–0.3$) (Figure 5). All models met

TABLE 2 Regression coefficients of the best-fitting model (lowest AICc) (all regressions in Appendix S3) describing relationships between the set of hydrological (H = runoff + dry days) and catchment (C = elevation + anthropogenic impacts + salinity) predictors and both (A = H + C) sets of predictors, and Marxan site selection frequency when using only aquatic (Aq) or aquatic and terrestrial (All) taxa for Marxan site selection at 3 thresholds of taxa representation (50%, 75%, and 90%).[a]

Type of taxon and threshold	Intercept	Elevation	Elevation^2	Anthropogenic impacts	Salinity	Runoff	Runoff^2	R^2
Aq90 (A)	30.79	−0.89	0.02	−2.04		5.62	0.44	0.26
Aq75 (A)	24.03	−0.68	0.02	−1.74		4.24	0.34	0.26
Aq50(A)	18.12	−0.55	0.01	−1.23		3.14	0.25	0.27
All90(C)	15.45	−0.69	0.01	−1.91	−0.46			0.2
All75(C)	12.84	−0.58	0.01	−1.6	−0.35			0.23
All50(C)	10.73	−0.52	0.01	−1.13	−0.37			0.28

Abbreviations: Aq90/All90, Aq75/All75, and Aq50/All50, 90%, 75%, and 50% of aquatic or aquatic and terrestrial taxa, respectively, covered in this site selection.
[a]Only predictors included in at least 1 top model are included.
[b]Goodness of fit.
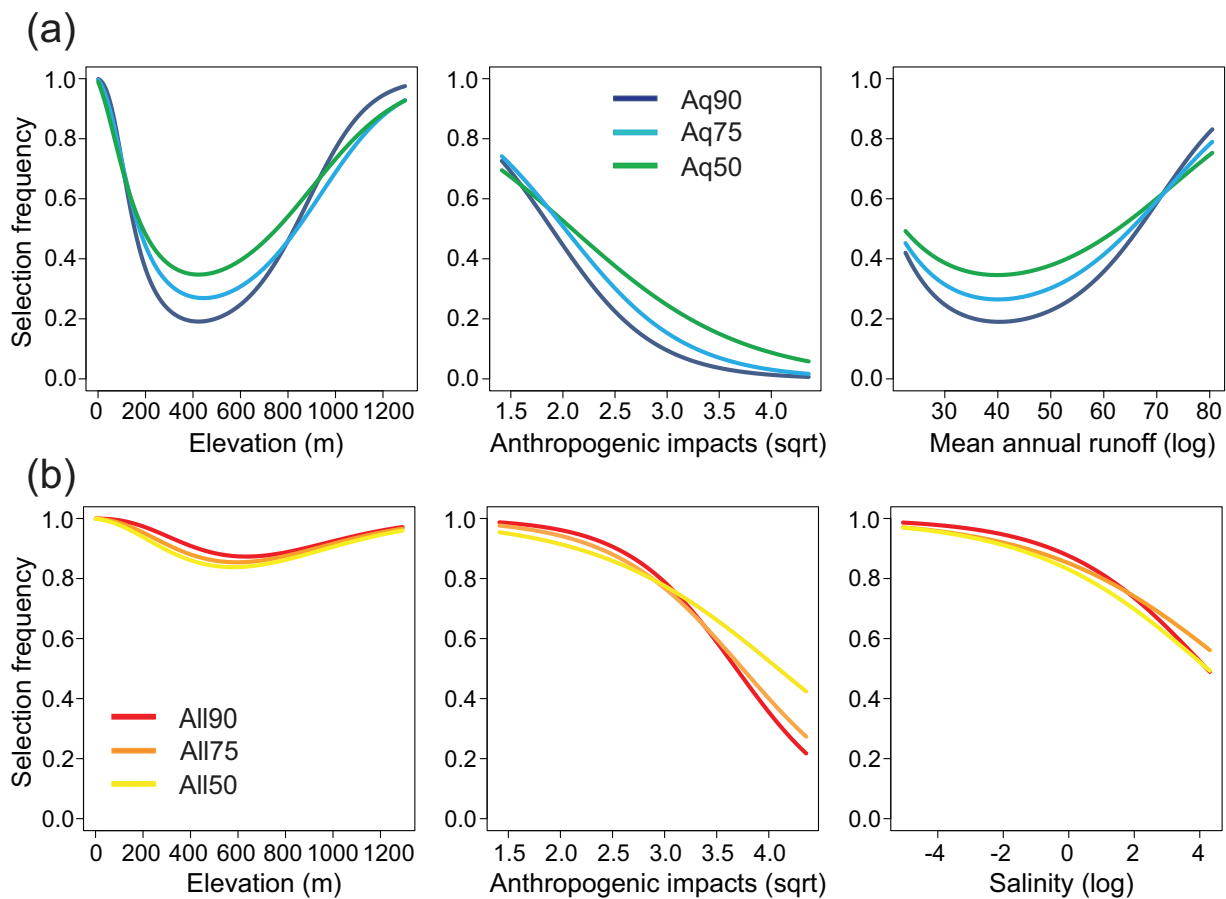
FIGURE 4 Results of the best regression model of Marxan site selection frequency, showing significant relationships with environmental variables when considering (a) only aquatic (Aq) and (b) aquatic and terrestrial (All) taxa selection at 3 thresholds of taxa representation (50%, 75%, and 90%)

normality and homoscedasticity assumptions (diagnostic plots in Appendix S4).

DISCUSSION

Our results showed that NPRS and their corridors are valuable habitats for aquatic and terrestrial taxa conservation (Datry et al., 2017). As expected, NPRS were more frequently selected than PRS to represent both aquatic and terrestrial taxa; aquatic taxa had a low potential as surrogates for terrestrial taxa; and site selection frequency in prioritization analyses (Marxan), and therefore their importance to achieving conservation targets, was determined by a combination of hydrological and non-hydrological gradients.
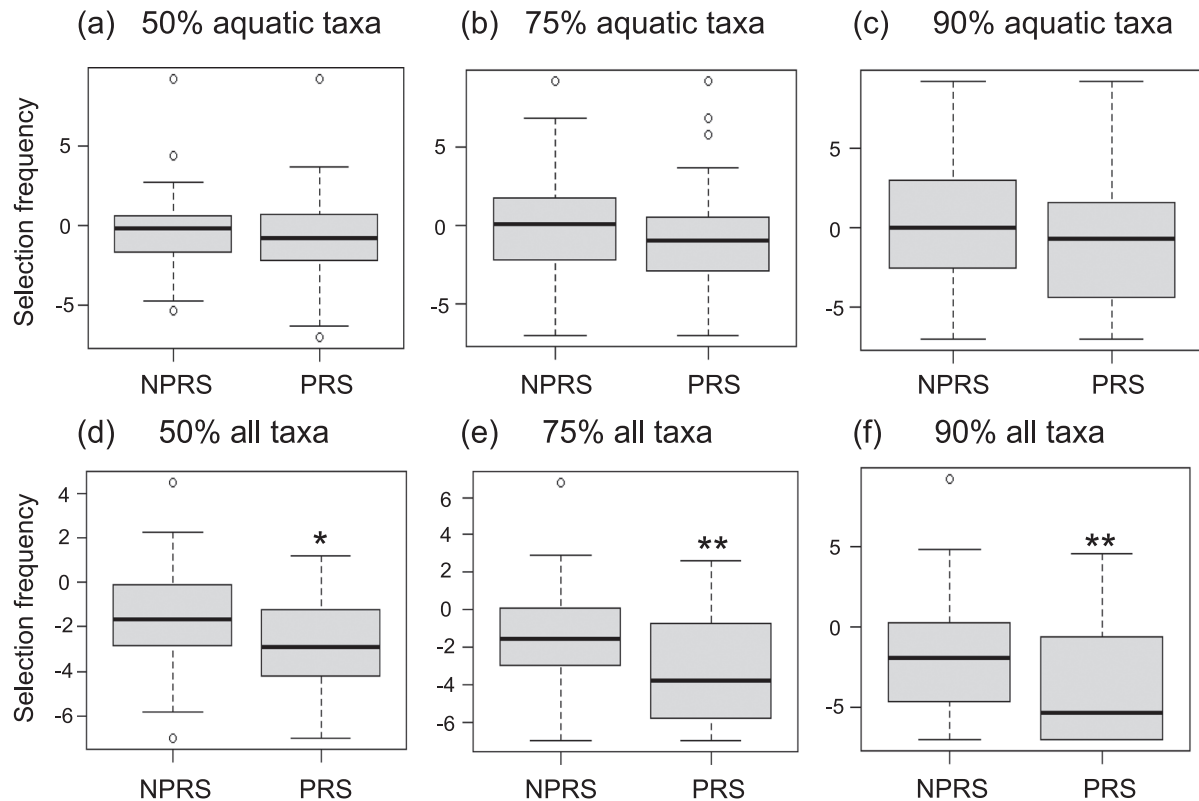
FIGURE 5 Comparison of Marxan site selection frequency (Mann–Whitney–Wilcoxon test, $*p < 0.05$, $**p < 0.01$) between perennial (PRS) and nonperennial (NPRS) rivers and streams when using (a, b, and c) only aquatic and (d, e, and f) aquatic and terrestrial taxa at 3 thresholds of taxa representation (50%, 75%, and 90%) (horizontal line, median; box ends, interquartile range; whiskers, observed maxima and minima; points, outliers)

Our study contributes to the quantification of the long-claimed conservation value of NPRS (Acuña et al., 2014). We also demonstrated the importance of accounting for both aquatic and terrestrial taxa when assessing the conservation value of rivers and their riparian zones, particularly for NPRS. Priority sites for conservation we identified based on only aquatic taxa (as it is commonly done in freshwater assessments [Hermoso et al., 2009]) tended to underrepresent terrestrial taxa, which tended to miss their representation targets, and NPRS, which were less frequently selected than PRS. In addition, our models showed that both natural and anthropogenic factors influenced the selection of priority sites for conservation. Thus, we call for explicitly incorporating hydrological gradients from PRS to highly intermittent NPRS and considering both aquatic and terrestrial taxa associated with watercourses in biodiversity conservation plans.

Conservation value of nonperennial watercourses and surrogacy potential of aquatic taxa

Aquatic taxa were not good surrogates for terrestrial biodiversity associated with NPRS or PRS in our river network. Terrestrial taxa were underrepresented in solutions identified using aquatic biodiversity only. These results align with previous

studies that recognize the biodiversity value of dry channels for terrestrial groups and the need to explicitly consider terrestrial plants (Westwood et al., 2021), carabid beetles (Bunting et al., 2021), and vertebrates (Sánchez-Montoya et al., 2022) when assessing the conservation value of freshwater ecosystems. The inclusion of terrestrial taxa resulted in a higher selection frequency of NPRS, which is evidence of the strategic conservation value of these dynamic wet–dry habitat mosaics and their ability to complement the biodiversity of PRS (Datry et al., 2016).

The capacity of NPRS to support both aquatic and terrestrial biodiversity in semiarid catchments reflects their spatiotemporal variability in hydrological conditions (watercourse reaches shift from wet to dry phases and vice versa [Cid et al., 2017; Price et al., 2021]). Despite their lower local aquatic richness compared with PRS (Soria et al., 2017), NPRS host rare and specialist species that contribute to increased regional diversity in invertebrates (Belmar et al., 2019; Sánchez-Montoya et al., 2020), riparian vegetation (Bruno, et al., 2016), and terrestrial vertebrates (amphibians, reptiles, birds, and mammals) (Sánchez-Montoya et al., 2017, 2022). Moreover, alpha and beta diversity may be higher in NPRS than PRS not only for aquatic communities (Stubbington et al., 2017), but also for some terrestrial communities (e.g., ground-dwelling arthropods) due to the important role of NPRS corridors in harboring more unique species than adjacent terrestrial habitats (Sánchez-Montoya et al., 2020).

We detected a convex relationship between runoff, flow intermittence, and site selection frequency. This relationship indicates that Marxan selected combinations of perennial sites with high runoff that had high alpha diversity and others with nonperennial flow and low runoff that harbored rare taxa. This combination thus aligns with the principle of complementarity, which is incorporated in Marxan's prioritization approach (Margules & Pressey, 2000). Similar patterns have been found for wetlands in Patagonia, where the inclusion of nonperennial sites in conservation priorities increased regional diversity due to the occurrence of taxa adapted to recurrent drying (Epele et al., 2021).

Our results suggest that NPRS can contribute greatly to catchment-scale conservation value, but flow intermittence had a limited effect on site selection compared with other environmental variables, such as anthropogenic impacts, elevation, and salinity. This result might reflect contrasting ecological responses across different terrestrial and aquatic groups, wherein the latter are much more dependent on water availability. Thus, under the all-taxa scenario, we needed a complementary set of sites where both aquatic and terrestrial taxa were represented. This forced Marxan to include both sites that were permanent, for the strictly aquatic taxa, and intermittent, where terrestrial species could also be covered. As a result, flow intermittence was not the most important variable explaining selection frequency. Although this metric has been widely used to effectively capture spatial differences in riparian vegetation and aquatic macroinvertebrates (Bruno et al., 2014; Sánchez-Montoya et al., 2007), other metrics, such as the maximum duration of the dry period or the frequency of drying events, can also be relevant (Arias-Real et al., 2021; Crabot et al., 2020; Pineda-Morante et al., 2022; Sánchez-Montoya et al., 2018). The use of in situ hydrological measurements (e.g., data loggers) can better capture recent (e.g., duration of the last dry period) and annual (e.g., annual drying duration and frequency) variability (Arias-Real et al., 2021; Pineda-Morante et al., 2022), but long-term metrics that represent average conditions in the last decades, such as the mean number of dry days per year and proportion of years with no flow, are particularly relevant and indicated when sampling sites have been surveyed across several years (Bruno, Gutiérrez-Cánovas, Velasco, et al., 2016a; Bruno, Gutiérrez-Cánovas, Sánchez-Fernández, et al., 2016b; Belmar et al., 2019; Stubbington et al., 2022). Finally, that biodiversity surveys were conducted at the end of the wet phase might also have masked flow intermittence effects on biological groups. Future studies should integrate long-term and seasonal hydrological variation of NPRS to better understand their aquatic and terrestrial conservation value.

Non-hydrological variables influencing site selection

Elevation and site selection frequency had a convex relationship; sites at the extremes of the gradient were selected more frequently. This pattern reflects the different affinity of species for the environmental conditions occurring over elevational gradients (Gutiérrez-Cánovas et al., 2013). From a complementarity point of view, intermediate elevations could enable greater biodiversity conservation because they support high-diversity communities, including species from both extremes (Guareschi et al., 2012). However, as elsewhere, our high-elevation watercourses could harbor rare and unique taxa due to a combination of spatial isolation, relatively pristine condition, and particular environmental factors (Finn et al., 2011; Tierno de Figueroa et al., 2010). In contrast, low-elevation streams offer more stable environmental conditions and low resistance to dispersal (Brown & Swan, 2010; Jamoneau et al., 2018). Therefore, the extremes of the elevational gradient can complement each other in terms of biodiversity representation, and this could explain why they were more frequently selected by Marxan.

Site selection frequency and anthropogenic impacts and salinity were significantly negatively related. The negative relationship with anthropogenic impacts was expected because the communities of disturbed sites are usually nested within those of relatively pristine sites (Gutiérrez-Cánovas et al., 2013), thereby offering lower conservation value. The declining frequency of site selection as salinity increases aligns with the decline in local species richness observed along salinity gradients in rivers worldwide (Cañedo-Argüelles et al., 2013), particularly in Mediterranean catchments (Gutiérrez-Cánovas et al., 2019), including our study area (Suárez et al., 2017). Similarly, the negative relationship between salinity and site selection frequency may reflect limitations of our analyses. Because Marxan tends to maximize the number of taxa represented in the protected site network, the reduced pool of specialists that occurred in saline watercourses might have biased site selection toward freshwater sites, even at the upper taxa conservation threshold (90%). We only considered a limited proportion of all potential taxa inhabiting these systems. We recognize the very restricted distribution range, rarity, uniqueness, and habitat specialization of saline biota (Millán et al., 2011) and thus the high conservation value of saline rivers, and our observed negative correlation between salinity and site selection frequency should be considered cautiously. Further analyses accounting for the relative proportion of endemism and rarity are needed to develop site selection procedures that adequately represent biodiversity in saline rivers (Sánchez-Fernández et al., 2008).

Although our compiled data set included data from multiple studies not specifically designed to meet our study aims, it represents the best compilation of information on the catchment, including aquatic and terrestrial taxa extensively distributed throughout NPRS and PRS. Spatial and temporal biases in data must be taken into account when interpreting the outcomes of spatial prioritization tools. Although the spatial coverage of our data was not balanced among taxonomic groups (which represented different number of sites), they adequately covered the main natural and anthropogenic gradients (Appendix S1). When running Marxan, use of complete, catchment-wide taxa distributions is recommended because unequal sampling could be a major drawback to identifying a set of river reaches for conservation or to designing a protected area network (Ardron et al., 2010). However, our results are not intended to be used directly for conservation planning in particular areas. Rather, they are

useful in demonstrating that aquatic taxa are not necessarily good surrogates of terrestrial taxa and that NPRS have biodiversity conservation value that complements that of PRS. We obtained consistent results when seeking to represent 3 different proportions (i.e., 50%, 75%, and 90%) of randomly selected taxa, reflecting the limited influence of potential taxonomic imbalance in our results.

The opportunistic nature of our data set introduced some temporal variability. To account for the influence of intra- and interannual variability in the study area (Belmar et al., 2011), biological data were collected under low-flow conditions and we used mean values of environmental variables representative of average conditions. Ultimately, the representation of multiple aquatic and terrestrial groups in different seasons (and thus in-channel conditions) in several years would be required to comprehensively and fully characterize the distribution of biodiversity in NPRS. However, such data remain scarce, in particular for the terrestrial communities associated with NPRS (Datry et al., 2017; Stubbington et al., 2018). Future research could build on our results by completing the spatiotemporal dimension of this data set (e.g., through species distribution models) through establishment of a set of sites at which multiple groups of organisms are collected and incorporation of a wider gradient of drying duration and predictability, as well as NPRS in other climates and regions.

Management and conservation implications

Our results could support the development of novel strategies to improve terrestrial and aquatic biodiversity conservation, in particular through the incorporation of terrestrial taxa and NPRS into river conservation schemes. Although we found a higher site selection frequency for NPRS for aquatic and terrestrial communities, NPRS are usually underrepresented in protected area networks (Stubbington et al., 2018). Only 1 NPRS, the upper part of the Chícamo stream (9.37 km long of a total of 184.61 km protected), has national designation as a freshwater protected area in the catchment. Given their biological value and low representation in conservation schemes (Abellán et al., 2007; Fritz et al., 2017), saline NPRS should be incorporated into river conservation networks. Overall, our outcomes align with previous studies illustrating the high value, poor management, and low legal protection of NPRS (Sills et al., 2018; Skoulikidis et al., 2017).

Some taxonomic groups are poorly represented in the Habitats Directive (e.g., freshwater fish and molluscs [Hermoso et al., 2019]), and the Natura 2000 network provides low coverage for a vast number of aquatic species (Hermoso et al., 2015), despite including hotspots of aquatic threatened species (Sánchez-Fernández et al., 2021). Moreover, Natura 2000 is spatially biased, covering predominantly the least disturbed areas (e.g., mountainous and less populated regions [Hermoso et al., 2015]). Therefore, future expansion of the protected area network should account for these taxonomic and spatial biases to close the taxonomic gap observed. The recently adopted EU Biodiversity Strategy for 2030 (European Commission, 2020) represents a window of opportunity for closing this conservation gap because it aims to extend the network of protected areas. Although there are important barriers to overcome, such as the outdated lists of species and habitats of conservation concern that guide the designation of protected areas (Hermoso et al., 2019), creating a larger network of protected areas represents an opportunity to improve the conservation of NPRS if adequately planned and managed. Our data support the inclusion of naturally stressed watercourses in conservation networks, particularly in semiarid regions with NPRS that exhibit long dry periods, and point to the need to cross ecosystem boundaries to protect a wider fraction of biodiversity.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.