

ORIGINAL ARTICLE

Prolonged flow intermittency undermines the habitat potential of forested landscapes for a stream-dwelling dragonfly

Judit Fekete^{1,2}  | Gábor Várbiro²  | Júlia Szeles²  | Tamás Bozókí²  |
Bálint Pernecker³  | Zoltán Csabai^{3,4}  | Pál Boda² 

¹Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary

²HUN-REN Centre for Ecological Research, Institute of Aquatic Ecology, Debrecen, Hungary

³Department of Hydrobiology, University of Pécs, Pécs, Hungary

⁴HUN-REN, Balaton Limnological Research Institute, Tihany, Hungary

Correspondence

Pal Boda, HUN-REN Centre for Ecological Research, Institute of Aquatic Ecology, Bem square 18/c, Debrecen, 4029-Hungary.
Email: boda.pal@ecolres.hu

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Abstract

1. Understanding how land use and variability of the hydrological regime jointly shape species distributions is essential for the conservation of aquatic insects in increasingly intermittent streams.
2. We investigated how flow intermittency influences the relationship between land use and the occurrence probability of *Cordulegaster heros* in a drying river network.
3. Field surveys were conducted at 42 stream sites in southwestern Hungary over a two-year period. We combined species presence-absence data with land use variables and hydrological proxies. Statistical analyses included decision tree modelling and binomial generalised linear models.
4. *C. heros* was associated with forested landscapes and absent from sites with prolonged zero-flow periods or high agricultural land use. Occurrence probability declined markedly when forest cover was low or when dry periods were extended in duration.
5. Although *C. heros* larvae can tolerate short-term drying by burrowing into sediments, prolonged flow intermittency and reduced landscape connectivity may limit both survival and recolonisation. Our findings underscore the need for conservation strategies that jointly address land use and hydrological conditions to counter the rising flow intermittency expected with ongoing climate change.

KEYWORDS

dragonfly distribution, hydrological regimes, intermittent streams, larval development, species persistence

INTRODUCTION

The distribution of freshwater macroinvertebrate species is shaped by a complex interplay of abiotic and biotic factors that determine their presence. The species distributions are dynamic, reflecting the constantly changing environmental conditions (IPCC, 2021). For dragonflies (Odonata), which have aquatic larvae and terrestrial adults, two key environmental factor groups shape their local occurrence, and through this, their distribution: (i) the key biotic and abiotic instream

factors such as riffle-pool structure, microhabitat composition, flow regime, food availability, predator presence, instream macrophytes and human-induced disturbances (Boda, Bereczki, Pernecker, et al., 2015a; Holuša et al., 2023; Holuša & Holušová, 2022; O'Malley et al., 2020; Pernecker et al., 2020), all of which play a crucial role in the development of the larva and the emergence of the adult (Boda, Bereczki, Ortmann-Ajkai, et al., 2015b); (ii) characteristics of the surrounding terrestrial and riparian habitats, which not only influence the emergence process but also affect the larval habitat indirectly through

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processes such as nutrient input, shading and other ecological interactions (Balzan, 2012; de Knijff, Billqvist, van Grunsven, Allen, et al., 2024a; de Knijff, Billqvist, van Grunsven, Vinko et al., 2024b). Due to their limited mobility, Odonata larvae are confined to small areas and are highly dependent on the local environment. By contrast, adult dragonflies are highly mobile, and their distribution is strongly influenced by the broader landscape surrounding aquatic habitats (Dolný et al., 2021; Holuša et al., 2023). This environmental context highlights the complexity of the environment and its sensitivity to both local and land use factors (Dolný et al., 2014). For effective conservation of dragonfly species, it is crucial to understand how these multi-scale drivers interact to shape species distributions and occurrence in a particular habitat.

Land use practices can significantly alter landscape conditions, impacting freshwater systems and the organisms they support (Allan, 2004; Feld et al., 2016; Shen et al., 2024). Among these, agricultural activities frequently introduce pollutants, degrade water quality, and reduce habitat suitability for Odonata, by limiting breeding and foraging opportunities and decreasing invertebrate prey diversity (Bond et al., 2006; de Knijff, Billqvist, van Grunsven, Allen, et al., 2024a; Huynh et al., 2020). Adequate habitats that are not heavily modified by human activities provide essential resources such as food, shelter and breeding sites, and play a crucial role in shaping the distribution of odonates through species-specific preferences (Dolný et al., 2014, 2021). However, the habitat composition is influenced by broader streamside landscape changes. For example, alterations in land use can degrade or eliminate habitats in reach scale, rendering them unsuitable for species. Thus, the optimal conditions for their presence depend on the combined favourability of land use at the landscape level, and hydrological conditions at the reach scale (García-García et al., 2017). In parallel, climate-induced changes, such as the growing frequency and intensity of flow intermittency, further threaten aquatic ecosystems (Lucas-Picher et al., 2024; Palmer et al., 2008; Vinko et al., 2023). These disruptions alter hydrological regimes, reducing water availability and affecting microhabitat conditions for aquatic organisms. For many Odonata species, particularly those dependent on perennial flow, increased flow intermittency can interrupt larval development, reduce survival during dry periods, and limit the availability of suitable oviposition sites (Pernecker et al., 2020; Vinko et al., 2023). Species with such long larval development as the model species of this study, the Balkan Goldenring (*Cordulegaster heros* Theischinger, 1979), can be especially vulnerable, as extended dry phases can exceed their physiological tolerance and lead to local disappearance.

Cordulegaster heros is endemic to central and southeastern Europe. It is a Natura 2000 species of community importance listed in Annex II and IV of the EU Habitats Directive (EC, 1992), as well as a strictly protected dragonfly in Hungary (VM, 2012). It is listed in Annex IV of the Bern Convention, and on the IUCN Red List. The current IUCN conservation status of the species is Least Concern (LC) (Vinko et al., 2023). It was previously listed as Near-Threatened (NT) (Boudot, 2010; Boudot, 2020), primarily due to data deficiency rather than observed population decline (Vinko et al., 2023). It occurs

besides Hungary in Albania, Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czechia, Greece (mainland), Italy (mainland), Montenegro, North Macedonia, Romania, Serbia, Slovakia, Slovenia and Ukraine (Vinko et al., 2023). Larvae prefer cool, slow-flowing parts of shaded first and second-order headwater streams, and finer particulate streambed material, where they usually burrow into the sediment (Boda, Bereczki, Pernecker, et al., 2015a; Lang et al., 2001). The detailed ecological preferences of the species were assessed by Pernecker et al. (2020). *C. heros* is considered sensitive to habitat destruction, such as stream modifications, deforestation and water extraction for human use (Vinko et al., 2023). Additionally, climate change-driven droughts could also threaten its populations, especially in the southern Balkans. Other pressures include agricultural activities, pollution, logging, forest fires, dams and planned hydro-plants (Vinko et al., 2023). Despite its importance for nature conservation, only a few studies have focused on the drying-resistant mechanisms of the species (Pernecker et al., 2020; Vilenica et al., 2022), and no research to date has linked flow intermittency and the occurrence of this species.

While climate change increases the bioclimatic suitability of certain areas for *C. heros* (Fekete et al., 2023), land use and flow intermittency might determine actual local distribution patterns. Our study aims to refine the understanding of reach-scale habitat requirements of *C. heros* by examining patterns observed across multiple sites within a drying river network. Specifically, we investigate how flow intermittency influences the relationship between land use and the probability of species occurrence. We predicted that prolonged flow intermittency substantially limits the occurrence of *C. heros*, even in forested landscapes generally considered optimal for the species.

MATERIALS AND METHODS

Study area

This research focused on a drying river network in the Mecsek Mountain range of southwestern Hungary, specifically the streams within Bükkösd and Bicsérd sub-catchments within the Fekete-víz catchment (Figure 1). These streams flow through hilly terrain, with bedrock composed predominantly of calcareous material or red sandstone, and their sediments range from fine to coarse in grain size. A hydrologically diverse network of streams that flow through a landscape characterised primarily by various types of sedimentary bedrock materials (mainly limestone, loess and red sandstone) creates a mosaic of perennial and intermittent stream sections. The whole catchment consists of forest (81%), grassland (8%), and agricultural areas (6%) and less than 4% artificial (urban). These proportions were calculated using QGIS 3.16 (QGIS Development Team, 2021), based on data from the Ecosystem Map of Hungary (NÖSZTÉP, 2019; Tanács et al., 2022). In forested areas, the dominant tree taxa include beech (*Fagus* spp.), oaks (*Quercus* spp.), poplars (*Populus* spp.), birch (*Betula* spp.), and black locust (*Robinia pseudoacacia*). Aquatic macrovegetation is consistently sparse or absent across all sampling sections, with vascular

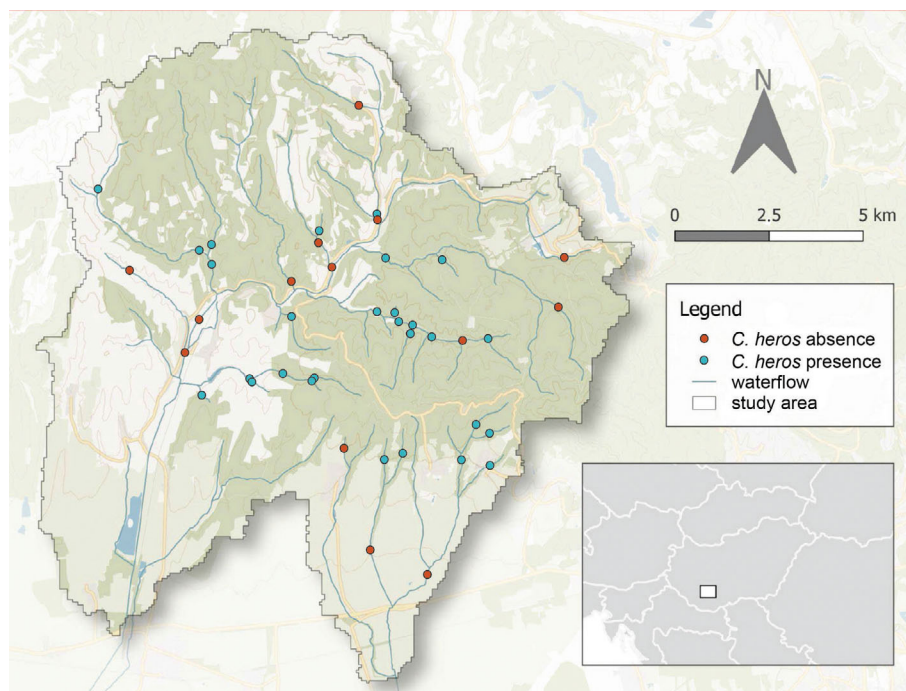


FIGURE 1 The study area is within the Bükkösdí-víz catchment, located in the Mecsek mountains in southwest Hungary (blue circles: Presence of *C. heros*, red circles: Absence of *C. heros*).

macrophytes occurring only occasionally. Although substrate composition varied slightly among stream sections depending on their network position, all sites featured microhabitat conditions considered optimal for *C. heros* occurrence, characterised by low to moderate heterogeneity, and a higher proportion of fine substrates (Boda, Bereczki, Pernecker, et al., 2015a; Lang et al., 2001). Except for a few sites located in the middle and lower sections of the main stem of the Bükkösdí-víz, all streams and studied sections are near-pristine, hydro-morphologically unmodified and provide microhabitat conditions potentially suitable for the species' larvae. Sampling sections (hereafter referred to as sampling sites) were strategically positioned in relation to stream confluences, representing key longitudinal segments of the catchment from headwaters to lower reaches. A total of 42 sampling sites were selected, overlapping the known habitat range of *C. heros* (Figure 1).

The study area is located within the temperate climate zone, with a slight sub-Mediterranean influence, leading to a moderately cool and dry climate. The average annual temperature in the study region, based on data from 2002 to 2015, is 11.1°C, with an annual average precipitation of 732.3 mm (Ács et al., 2015; Mezősi, 2017). During the study period, the mean annual temperatures were 10.9°C (2021), 12.1°C (2022) and 12.3°C (2023), while the total annual precipitation was 556.6, 466.4 and 773.1 mm, respectively (Meteorological Database, HungaroMet). According to climate data from 1991 to 2020, the region surrounding the sampling site is characterised by warm summers (mean seasonal temperature: 21.4°C; mean seasonal precipitation: 72.3 mm) and cold winters (mean seasonal temperature: 1.2°C; mean seasonal precipitation: 38.7 mm). Spring temperatures are

moderate (seasonal mean: +11.6°C; 53 mm precipitation), and autumn shows a gradual temperature decrease (seasonal mean: +11.6°C; 60.3 mm precipitation) (OMSZ, 2024). According to the latest models of the Köppen-Geiger climate classification (Beck et al., 2023), most of the study area falls within the Cfa zone (warm temperate), characterised by warm summers, mild cold winters and moderately seasonal precipitation. Between 1981 and 2020, the mean annual temperature in Hungary increased by 1.7°C, with an increase of 1.5°C in the southwestern region, including the study area. From 1901 to 2020, annual precipitation in the study area decreased by 10%. In addition, the number of days with precipitation decreased by 17 days during this period, whereas the longest dry period increased by 4 days (IEA, 2021). In line with climate change, regional temperatures are rising, and the study area is becoming drier, making it one of the most drought-prone counties and susceptible to the expected effects of drying in Hungary (Buzási et al., 2021).

Biotic sampling

Macroinvertebrate samples were collected using the standard kick-and-sweep method with a 1-mm mesh, 25 × 25 cm frame net, following a multihabitat approach proportional to substrate composition. Each sample consisted of 10 sample units collected along a 100-metre stream reach. Each sample unit covers an area of 0.25 × 0.25 m; thus, the total sampling area was 0.625 m² (more info in Bozóki et al., 2024). Samples were sorted in the field, and all of the *C. heros* larvae found in the sample were counted and recorded; however, for

the analyses, we used presence–absence biotic data (Boda et al., 2025). We defined species presence as the confirmed detection of *C. heros* during systematic surveys and considered the species absent when it remained undetected despite extensive and methodologically robust monitoring. The larvae were then carefully returned to their habitat; as a result, none of the individuals were harmed. Simultaneously with the biotic sampling, microhabitat composition ratios were documented during sampling, allowing quantification of the microhabitat composition at the sampling sites (Table S1).

Macroinvertebrates were sampled altogether nine times, in every season from spring 2021 until spring 2023 (May, August and September 2021; February, May, August and September 2022; February and May 2023). The samples were collected in the presence of surface water (flowing or pool phase), but we did not collect samples from dry streambeds.

Hydrological data

At each sampling site, a HOBO U20L-04 Water Level Data Logger was deployed to continuously measure and record water presence within the streambed over a two-year period (May 2021–May 2023). From the raw hydrological data, key flow intermittency proxies were calculated regarding the whole two-year period of the sampling campaign: the average duration of dry periods in days (average zero runs), the longest consecutive dry periods in days (longest zero runs), the number of consecutive dry periods over 30 days (long zero runs), the number of consecutive dry periods (zero runs) and the total number of dry days (zeros) recorded during the sampling period. These proxies provided valuable insights into the temporal variability of water availability within the stream, reflecting the seasonal and annual patterns of flow intermittency that characterised the hydrological conditions of the river network over the entire two-year sampling period. Based on these hydrological data, 31 of the 42 sampling sites were classified as intermittent, and 11 as perennial.

Land use data

In order to analyse the impact of land-use data on the distribution of species on a catchment scale level, at first, a Digital Elevation Model (DEM) of the study area was obtained from CGIAR-CSI© (2004–2024, CGIAR–Consortium for Spatial Information) and processed using WhiteboxTools to address topographic irregularities. Pit removal and sink-filling operations were performed to mitigate depressions that could potentially affect the hydrological analyses. Subsequently, flow direction algorithms were applied to delineate the direction of the water flow across the preprocessed DEM. Flow accumulation techniques were then used to assign values to each cell, representing the cumulative upstream flow contributing to that specific cell. Stream network delineation was conducted to identify concentrated flow paths, aiding the recognition of streams and drainage patterns. The resulting stream network was derived in raster format. The selected

sampling sites represent the potential outlet points and serve as targets for catchment delineation. For each sampling site, we delineated the contributing upstream catchment area, allowing us to calculate landscape-level variables. While the immediate riparian zones of most streams remained forested or partially vegetated, the broader catchment context often included substantial agricultural land use, which likely influenced the hydrological regime and ecological conditions. High-resolution (20 × 20 m) land-use data were sourced from the Ecosystem Map of Hungary (NÖSZTÉP, 2019). Land cover percentages were calculated for each individual catchment using data from the second depth category within the Ecosystem Map of Hungary database, encompassing agricultural areas (agriculture), forested regions (forest), grasslands (grassland) and artificial surfaces (urban). This categorisation ensured a robust dataset representing diverse land use types within the study area.

Data analyses

Principal component analysis

Principal Component Analysis (PCA) was performed to investigate the influence of land use and flow intermittency on *C. heros* presence and distribution (Boda et al., 2025). The PCA was performed to reduce dimensionality and identify key environmental variables (forest, grassland, agriculture, artificial (urban), average zero runs, longest zero runs, long zero runs, zero runs, zeros) contributing to species distribution patterns. The resulting principal components were plotted, and biplots were generated to illustrate the relationships between variables and principal components. Additionally, PCA results were visualised using scatter plots to provide a clearer representation of the variation in environmental factors associated with *C. heros* occurrence.

Binomial comparison

We used a binomial Generalized Linear Model (GLM) for modelling binary response variables (presence/absence). Binomial GLM allows the estimation of the relationship between predictor variables and the probability of presence or absence. The binomial logistic regression analysis was performed using the default 'glm' function (Bates et al., 2015). The model was fitted to the data (presence data and environmental predictors) and relationships between the predictor variables. Scatter plots were created for each predictive variable. The curve was added to the plot using the logistic regression method (method = "glm"), and the equation of the regression line is displayed.

Predictor variables included in the GLM were selected based on their significance in the Mann–Whitney *U* tests, which identified longest zero runs, average zero runs, zeros, forest cover and agricultural land use as key differentiating factors between presence and absence sites. We applied the Mann–Whitney *U* test to compare key hydrological proxies related to flow intermittency (longest zero runs, zeros, and average zero runs), and land use characteristics (forest and agriculture)

between sites with confirmed *C. heros* presence and those where the species was absent (Boda et al., 2025). Plots were visualised with significance values below $p \leq 0.05$.

All statistical analyses were carried out within the R statistical environment (R Core Team, 2024), utilising the packages factextra (Kassambara & Mundt, 2020) and FactoMineR (Lê et al., 2008).

Decision tree

A decision tree model was developed to classify the presence or absence of a specific condition based on multiple predictor proxies and variables, including zeros, average zero runs, longest zero runs, agriculture and forest. The model was implemented using the rpart package (Therneau et al., 2019), with the method parameter set to 'class' to specify a classification task. To mitigate overfitting, a complexity parameter (cp) of 0.07 was applied, along with constraints on node splitting criteria. Specifically, the minimum number of observations required for a node split (minsplit) was set to 2, while terminal nodes were required to contain at least 1 observation (minbucket). Additionally, the maximum tree depth (maxdepth) was limited to three levels to control model complexity and enhance interpretability.

Model performance was assessed using a confusion matrix comparing predicted classifications with actual values in the test dataset. The evaluation included key metrics such as accuracy, Kappa statistic, sensitivity, specificity and the p -value for assessing statistical significance. To facilitate interpretation, the decision tree was visualised using the rpart.plot and fancyRpartPlot functions (Williams, 2024), which provide enhanced graphical representations of tree structures. All data analyses were conducted using R, a language and environment for statistical computing (R Core Team, 2024).

RESULTS

The presence of *C. heros* larvae was registered at 21 out of the 42 sampling sites. In nine cases (42.9%), larvae were found at sites with permanent hydrological regimes, while in 12 (57.1%) cases, they were found at intermittent sampling sites. This corresponds to a detection rate of 81.8% in perennial streams (9 out of 11) and 38.7% in intermittent ones (12 out of 31).

The PCA analysis revealed distinct relationships between land use and flow intermittency proxies in explaining the presence of *C. heros* (Figure 2). The first two principal components (PC1 and PC2) accounted for 35.9% and 25.8% of the variance, respectively. Key contributors to PC1 included the longest dry periods (longest zero runs), the mean of dry periods (average zero runs) and flow intermittency (zeros). For PC2, notable contributors included forest cover and flow intermittency proxies as long zero runs and zero runs. Sampling sites where *C. heros* was present (green points) tended to cluster in areas characterised by longer wet phases and higher forest cover. By contrast, sites with higher agricultural land use and shorter wet events were associated with the absence of the species.

Based on the inset barplots, the proxies longest zero runs, average zero runs, and zeros exhibited the highest and most significant contributions to PC1. These proxies were primarily related to flow intermittency, highlighting their strong influence on the first principal component. By contrast, for PC2, the longest zero runs and forest cover were the dominant contributors. These findings emphasised that the flow intermittency variable played a major role in PC1, while PC2 was influenced by a combination of hydrological and land use characteristics.

Mann–Whitney U tests revealed significant differences between sites with and without *C. heros* in key hydrological proxies—longest zero runs ($W = 290$, $U = 137.0$, $p = 0.05$), zeros ($W = 291.5$, $U = 138.5$, $p = 0.04$), and average zero runs ($W = 290$, $U = 137.0$, $p = 0.05$)—with consistently lower values at sites where the species was present. Significant differences were also observed for land use variables: forest ($W = 125$, $U = 25.0$, $p = 0.03$) was positively associated with species presence, while a negative association was recorded with agricultural land use ($W = 312$, $U = 154.0$, $p = 0.01$). Binomial GLM analyses confirmed that the probability of *C. heros* presence decreased with increasing values of longest zero runs, zeros and average zero runs. The models also showed that the probability of species presence increased with greater forest cover (72% at 0.5 probability) and decreased with higher percentages of agricultural land use (10% at 0.5 probability) (Figure 3).

The decision tree analysis revealed that both flow intermittency and land use characteristics play significant roles in determining the presence or absence of *C. heros* (Figure 4). The most influential factor was the longest zero runs acting as a primary split, indicating that prolonged dry periods (over 94 days) strongly influence the species occurrence (Figure 4). Sites characterised by extended zero-flow conditions had a higher likelihood of species absence as seen in the left-most branch of the tree. Among sites where the longest zero runs were low (right branch of the tree), agricultural cover emerged as the next critical factor. Furthermore, at sites with lower agricultural impact, forest cover was identified as the next key variable, with less than 98 forested areas being associated with a greater probability of species presence (Figure 4).

DISCUSSION

Our study identified strong links between land use, flow intermittency, and the probability of *C. heros* occurrence across multiple streams in a drying river network. The species was generally recorded at sites with high forest cover and either permanent flow or dry phases lasting only a few weeks, based on field observations, although this threshold is not precisely defined in the literature. This pattern was further supported by a strong positive association between forest cover and the presence of *C. heros*, with persistence predominantly observed at sites where forest cover exceeded a 72% threshold of the catchment, as identified by our binomial GLM analyses. These findings highlight the importance of natural vegetation, particularly riparian forest cover, in supporting local populations of *C. heros*. Although the

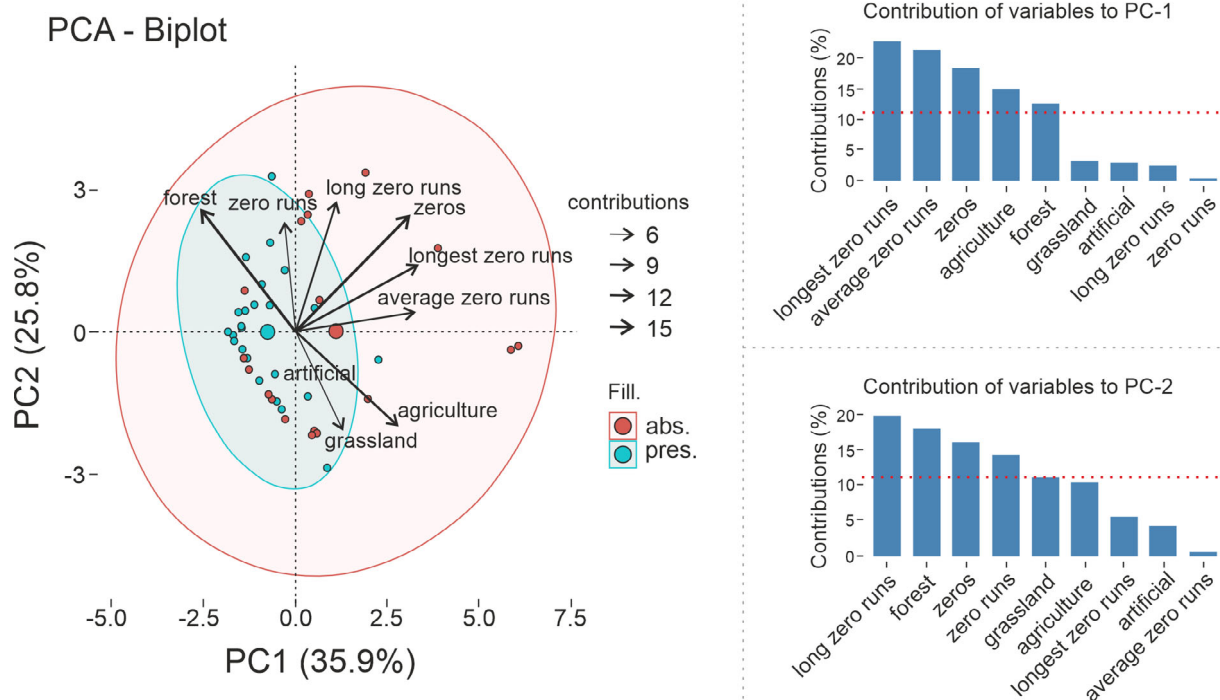


FIGURE 2 Principal Component Analysis (PCA) biplot illustrates the relationships between land use characteristics, flow intermittency variables and their influence on the presence of *C. heros*. Lengths and directions of the arrows indicate the strength and influence of the variables on site positions, respectively. Thicker and longer arrows indicate a greater contribution to the principal components. Red dots (abs) represent sampling sites where the species was not found, while blue dots (presence) indicate the occurrence of the species. The ellipses represent the grouping of sites based on the two-fill categories (0 and 1). The inset barplot displays the contributions of individual variables to PC1 and PC2, with a horizontal red dashed line marking the threshold for significant contributions.

importance of riparian vegetation for odonates in general has been suggested in previous studies (e.g., Balzan, 2012; Dolný et al., 2021), to our knowledge, this is the first study to quantify such a threshold specifically for *C. heros*.

The ecological value of forested riparian zones likely arises from multiple interacting mechanisms that help maintain conditions suitable for *C. heros*. Canopy shading moderates water temperature and reduces evaporation, leading to greater water retention in stream reaches during dry periods (Lang et al., 2001). This effect is particularly important in a drying river network, where unshaded reaches are more vulnerable to rapid desiccation. Furthermore, forests stabilise stream habitats by reducing erosion, filtering sediments and maintaining substrate heterogeneity (Gurnell et al., 1995). The level of structural complexity of riparian vegetation also contributes to successful emergence, as final larvae often climb onto tree trunks or woody vegetation to emerge and continue their life as terrestrial adults (Boda, Bereczki, Ortmann-Ajkai, et al., 2015b). These functions collectively underscore the importance of forested land cover for both larval development and life cycle completion.

By contrast with forested landscapes, agricultural land use had a strong negative effect on the occurrence of *C. heros*. Sites with higher

levels of agricultural land cover were consistently associated with species absence, indicating that land conversion to agriculture degrades habitat suitability. Agricultural activities often increase sediment and nutrient inputs into streams, which can lead to algal overgrowth, oxygen depletion, and changes in food web dynamics (Genito et al., 2002). Agricultural impacts can be multifaceted, with physical stress reducing benthic microbial biomass while increased nutrient availability enhances primary production and respiration efficiencies (Gücker et al., 2009). Although *C. heros* are predatory, shifts in trophic dynamics and reduced invertebrate diversity under eutrophic conditions may limit prey availability. These effects, combined with habitat simplification and increased disturbance, likely contribute to the reduced persistence of *C. heros* in agriculturally dominated landscapes, as defined by catchment-scale land use upstream of the sampling sites.

Although *C. heros* appears to tolerate moderate/low levels of flow intermittency (Pernecker et al., 2020), our findings indicate that prolonged or repeated drying events exceed the species' physiological and behavioural coping capacity. Larvae may temporarily survive short dry (a few weeks) periods by burrowing into moist sediments and retreating into the hyporheic zone (Pernecker et al., 2020), but this

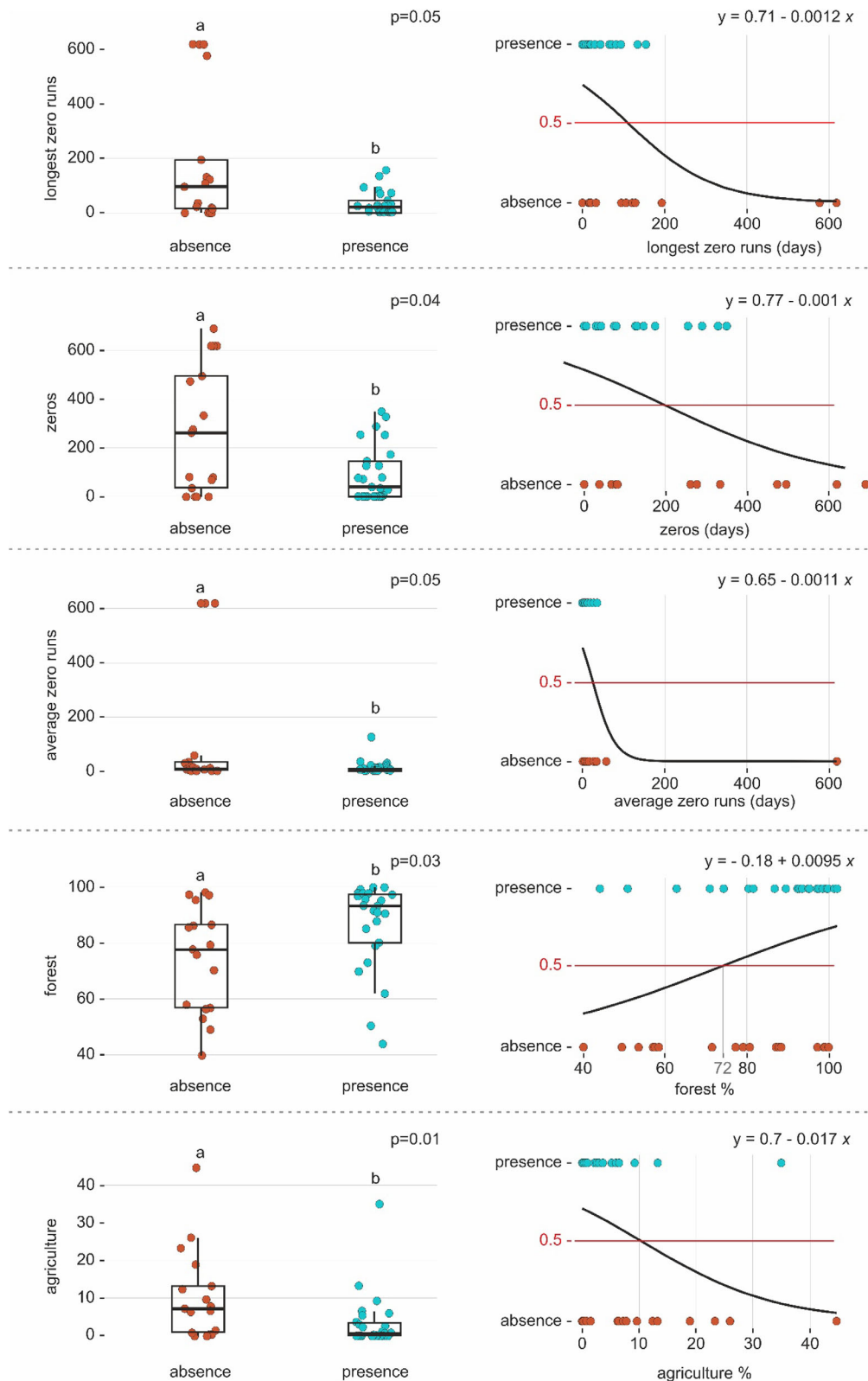


FIGURE 3 Pairwise comparison of *C. heros* presence and absence in relation to hydrological proxies using the Mann–Whitney *U* test (left) and binomial Generalised Linear Model (GLM) probability curves (right). The left panels display boxplots for the significant flow intermittency (longest zero runs, zeros, and average zero runs) and significant land use variables (forest and agriculture) (p -values ≤ 0.05). The right panels show the predicted probabilities of *C. heros* presence as a function of each variable. The y-axis represents the probability of *C. heros* presence, and the x-axis represents the timeline (number of days). The blue line is the fitted probability curves.

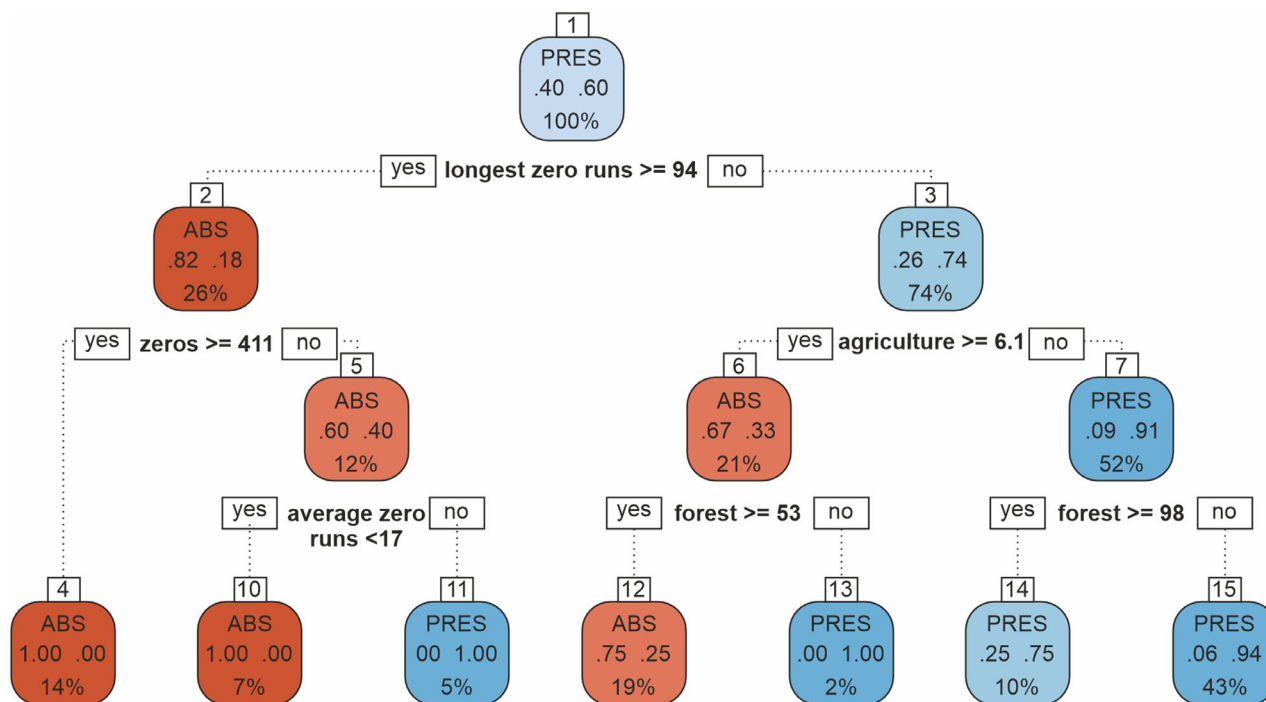


FIGURE 4 Decision tree showing the roles of land use and flow intermittency proxies in determining the presence (PRES) and absence (ABS) of *C. heros*. Nodes represent splits based on threshold values for the most important variables. The tree highlights the hierarchical importance of variables in determining *C. heros* occurrence, with darker nodes indicating higher predictive confidence. According to the model metrics, our tree shows high accuracy (0.881), Kappa (0.755), sensitivity (0.833), specificity (0.916) and low *p*-value (<0.001).

strategy might become ineffective under extended or frequent desiccation. As decision tree analysis revealed, flow intermittency proxies—particularly the longest dry periods—were the strongest predictor of species absence, even in otherwise favourable, highly forested environments. This suggests that hydrological conditions impose a hard threshold for persistence, beyond which habitat structure alone cannot compensate. Given the species' long larval development time (3–5 years), even a single extended drying phase may disrupt successful maturation, increasing the risk of local population collapse, and even a single year with prolonged drying may disrupt population continuity by interrupting development within a single cohort. Notably, the species was detected in over 80% of perennial streams but in less than 40% of intermittent ones, suggesting a clear preference for permanently flowing habitats. This supports the interpretation that while *C. heros* can tolerate short-term drying, its occurrence is markedly reduced under intermittent conditions. This detection rate disparity emphasises that intermittent sites are less consistently suitable and likely act as secondary habitats, contingent on local hydrological variability.

The persistence of *C. heros* at the catchment scale not only depends on local habitat conditions but also on the species' ability to recolonise suitable stream sections after local extirpations. Recolonisation following hydrological disturbance is essential for population maintenance, and depends on the presence of perennial refuges within the network and sufficient spatiotemporal connectivity between intermittent and permanent streams. However, this process is contingent on the presence of perennial refuges within the network

and sufficient spatiotemporal connectivity between intermittent and permanent streams. In fragmented landscapes, reduced connectivity may limit recolonisation opportunities, especially where suitable sites are sparse or isolated (Chalmandrier et al., 2025). In addition to recolonisation via dispersal, larvae may also survive drying by drifting downstream to more permanent water bodies, although the success of this strategy depends on the availability and proximity of perennial refuges. Nevertheless, the timing of adult emergence and oviposition in relation to dry phases could influence the species' ability to recolonise or maintain populations following rewetting. As we had no data on the developmental stage of the larvae encountered at intermittent sites, we cannot assess whether their presence reflects overwintering survival, delayed emergence or recolonisation by adults. While these strategies may contribute to population persistence, their relative importance remains to be clarified by future studies. The relatively high dispersal capacity of adult *C. heros* offers some compensatory potential, enabling individuals to locate and colonise suitable habitats beyond the immediate vicinity (Balázs et al., 2020). Maintaining or restoring dispersal corridors is therefore a key element in supporting population persistence under increasingly variable hydrological regimes and aligns with global priorities for safeguarding river connectivity as outlined in freshwater biodiversity recovery frameworks (Tickner et al., 2020). However, the specific characteristics of effective dispersal corridors for *C. heros* remain unknown, highlighting a clear research gap with important implications for targeted conservation planning.

In summary, our findings suggest that the presence of *C. heros* in drying river systems is shaped by both landscape characteristics and

local hydrological conditions. Forested areas support occurrence, but their effect is limited when streams experience frequent or prolonged drying. The spatial arrangement of suitable sites and their connectivity may further influence where the species can persist. These insights underscore the importance of broad-scale, integrated conservation planning in intermittent stream networks.

CONCLUSION

This study provides new insights into the factors shaping the local distribution of *C. heros* in drying river networks. While forested landscapes are associated with a higher probability of species occurrence, their capacity to sustain viable populations is substantially reduced under conditions of prolonged flow intermittency. Our findings highlight that land use alone is not sufficient to ensure the survival of local populations when drying events become more frequent or extended. Instead, conservation strategies must address the combined effects of landscape structure and hydrological dynamics. As climate change continues to intensify flow intermittency in stream ecosystems, effective conservation will require integrated approaches that couple land use management with hydrological interventions aimed at mitigating drying risk. Although our findings focus on *C. heros*, the patterns observed may have broader relevance for other species inhabiting intermittent streams, particularly those with limited tolerance to extended dry periods.

AUTHOR CONTRIBUTIONS

Judit Fekete: Conceptualisation; investigation; writing – original draft; visualisation; methodology; formal analysis; data curation; writing – review and editing. **Gábor Várbiro:** Data curation; formal analysis; writing – review and editing; methodology. **Júlia Szeles:** Writing – review and editing; data curation; visualisation. **Tamás Bozoki:** Investigation; visualisation; writing – review and editing; data curation; methodology. **Bálint Pernecker:** Writing – review and editing; investigation; methodology. **Zoltán Csabai:** Conceptualisation; writing – review and editing; supervision. **Pál Boda:** Supervision; resources; conceptualisation; investigation; funding acquisition; writing – original draft; writing – review and editing; methodology; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used in this study are publicly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dfn2z35dw>.

AI ASSISTANCE STATEMENT

The authors confirm that the content of this manuscript, including the conceptualisation, methodology, analysis and drafting of the text, was entirely created by the authors. A large language model was used solely to improve grammar and language clarity. It did not contribute to the intellectual content, data interpretation or conclusions of the manuscript. The authors take full responsibility for the scientific integrity of the work.

ORCID

Judit Fekete  <https://orcid.org/0000-0001-5623-869X>

Gábor Várbiro  <https://orcid.org/0000-0001-5907-3472>

Júlia Szeles  <https://orcid.org/0009-0004-9571-6200>

Tamás Bozoki  <https://orcid.org/0009-0003-7510-3936>

Bálint Pernecker  <https://orcid.org/0000-0003-0167-697X>

Zoltán Csabai  <https://orcid.org/0000-0003-1700-2574>

Pál Boda  <https://orcid.org/0000-0002-1825-5744>

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SUPPORTING INFORMATION

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

Table S1. Documented microhabitat composition ratios (% values) averaged across all sampling dates for each sampling site. All additional data used in the analyses are available via the Dryad repository: <http://datadryad.org/share/st8sTn-VDBYxdSWmQaMznPtbCzEARQ3YZ0mVssvOKxY>.

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