

# Beyond pests: intermittent rivers as habitats for Thysanoptera and Scolytinae

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**Abstract** – Intermittent rivers are dynamic ecosystems increasingly affected by climate change which extends their dry phase and alters connectivity. Drying events create temporal dispersal corridors for terrestrial animals including pest taxa with potential agricultural and forestry impacts. We aimed to investigate dispersal of thrips (Thysanoptera) and bark (and ambrosia) beetles (Scolytinae) in the Mediterranean karst intermittent river Krčić, Croatia, during its dry phase by assessing spatiotemporal distribution across habitats, reaches and times of day as well as the wind effect on their activity density. Insects were sampled using cross-vane window traps in riparian and dry riverbed habitats at upper and lower reaches. Traps were emptied every 12 h over seven days in July 2021, with wind continuously monitored. Thysanoptera activity density was significantly higher in the upper reaches and during the day; light wind enhancing their dispersal, but they showed no clear habitat preference. Scolytinae preferred riparian habitat relative to the dry riverbed, likely due to differences in environmental conditions, such as temperature, light intensity and humidity. While these taxa are commonly studied in relation to their host plants, this study highlights their ecology, contributing to a better understanding of how prolonged dry periods in intermittent rivers affect biological communities.

**Keywords:** Dispersal / dry riverbed / riparian habitat / thrips / bark beetles

## 1 Introduction

Intermittent rivers and ephemeral streams (IRES) are freshwater habitats that intermittently cease to flow and/or dry at some point along their course, harbouring different aquatic, semiaquatic, and terrestrial organisms (Datry *et al.*, 2017). IRES occur worldwide, and their spatial and temporal extent is expected to increase due to climate change (Palmer *et al.*, 2008). The summer drying maxima are expected to shift earlier in spring, with longer dry periods and more rivers shifting from perennial to intermittent flow (Mimeau *et al.*, 2025) affecting not only lotic habitats, but also dry riverbeds and adjacent riparian habitats. Dry riverbeds represent important temporary ecotones linking wet and dry phases, and transferring the energy and materials between aquatic and terrestrial

ecosystems (Steward *et al.*, 2012). They also serve as migration corridors for terrestrial and airborne organisms (Sánchez-Montoya *et al.*, 2016; Ružanović *et al.*, 2025). Riparian habitats are dynamic interfaces between terrestrial and aquatic systems, encompassing diverse mosaic of landforms and communities with high biodiversity (Singh *et al.*, 2021). They are characterised by enhanced nutrient availability due to regular flooding and closer access to groundwater, leading to higher primary productivity and beta diversity (Ramey and Richardson, 2017).

Thrips (Thysanoptera) and bark beetles (Coleoptera: Curculionidae: Scolytinae), commonly known as pests in forests and agricultural systems, have been found to inhabit various riparian habitats (Nicholls *et al.*, 2001; Atkinson and Riley, 2013). Thysanoptera naturally inhabit grasslands and shrublands but can enter greenhouses from native vegetation (Pizzol *et al.*, 2017) or infest orchards (Šimala *et al.*, 2017).

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They are typically associated with host plants and are mostly recognized for the economic damage through yield losses they cause in crops, partially through carrying tospoviruses (Mound, 2005). They also impact forests causing damage to tree foliage due to phytophagy (Marullo, 1990), contributing to the wood decay (Olsen and Midtgaard, 1996), or disease vectoring (Brownbridge *et al.*, 1999). Other than phytophagous opportunists, they can be mycophagous, pollenophagous, predators or ectoparasites on other arthropods (Kirk, 1987; Izzo *et al.*, 2002; do Vale Santos *et al.*, 2020). Their predatory behaviour is utilized in pest management as they can be used as biocontrol agents (Mound, 2011). In Europe, some Thysanoptera, such as *Thrips palmi* Karny, 1925, are monitored as quarantine species as they may be imported through shipments of cut-flowers, fruits and vegetables (Augustin *et al.*, 2012; Šimala *et al.*, 2023).

Scolytinae are important wood-decomposing insects feeding on plants (Kirkendall *et al.*, 2015). Many are secondary pests, typically invading cambial tissue of dead trees, although they can also infest stressed, weaker or even healthy living trees (Pernek *et al.*, 2019), degrading the timber value (Hrašovec *et al.*, 2008). However, Scolytinae also have important ecological roles as decomposers and “landscape engineers” (Raffa *et al.*, 2015). Moreover, they can enhance arthropod diversity in natural riparian ecosystems as other beetle species can secondarily inhabit their cavity system in host trees (Macedo-Reis *et al.*, 2016). Climate change, especially extreme temperatures and droughts, contributes to the Scolytinae outbreaks, which along with the resulting tree mortality can reduce forest carbon uptake (Kurz *et al.*, 2008). Significant impacts of Scolytinae outbreaks on ecosystems, economy, and society were reported for many European (*e.g.*, Hlásny *et al.*, 2021) countries. Managing Scolytinae populations requires a context-specific approach that differentiates between forests managed for different societal objectives (delivery of timber production vs. nature conservation), with responses spanning from non-intervention to active prevention of excessive population levels (Hlásny *et al.*, 2021). In Croatia, the Scolytinae outbreaks from 2003 to 2006, enhanced by high temperatures, drought, and inappropriate forestry measures, caused the decline and dieback of continental beech and fir forests (Hrašovec *et al.*, 2008). The above-mentioned damages to forests caused by Thysanoptera and Scolytinae resulted in these insects being included in forest and crops monitoring and management programs.

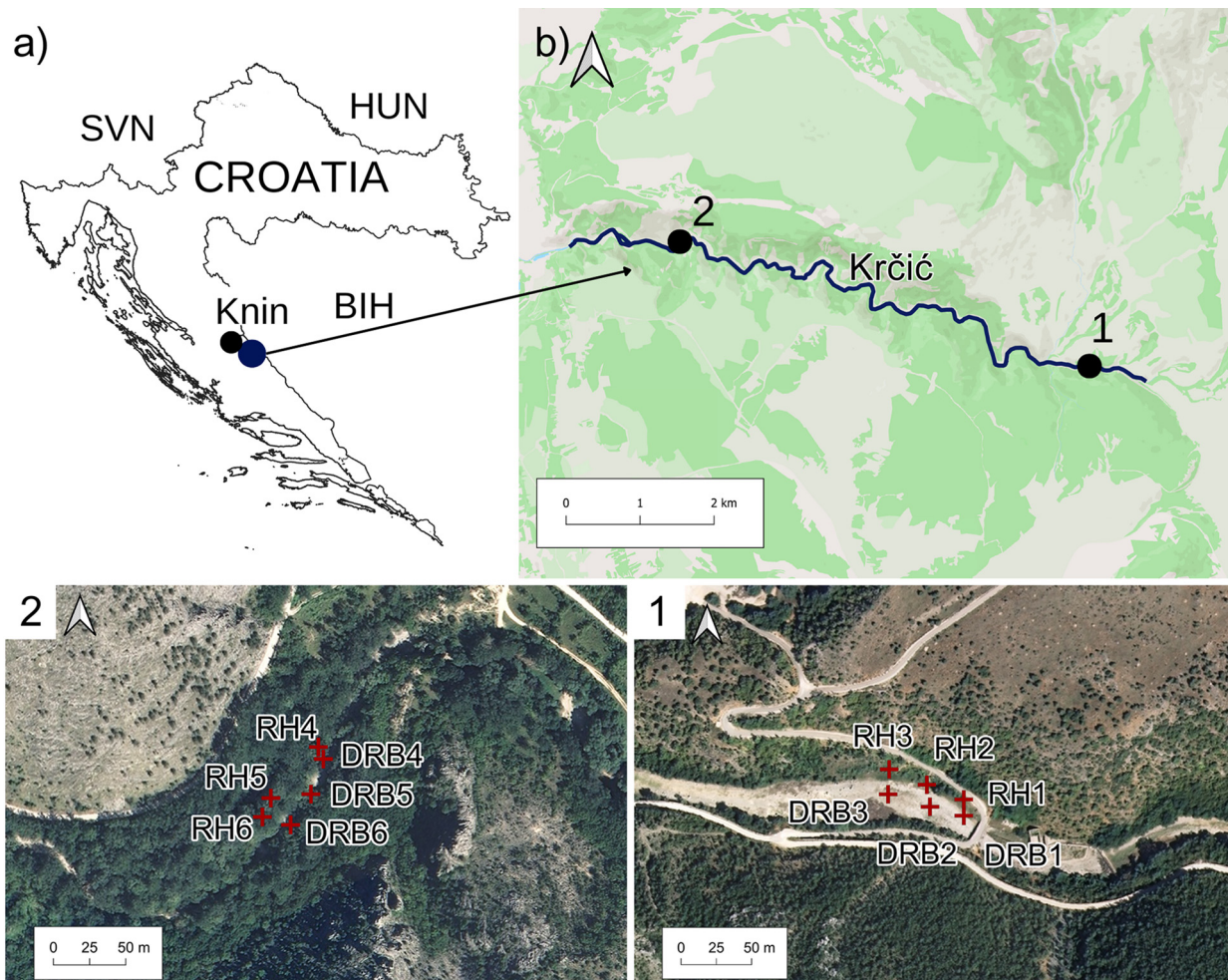
Thysanoptera disperse primarily through wind-assisted self-dispersal and human activity (Arévalo and Liburd, 2007). Although they are generally poor fliers with limited control of direction, wind can carry them over long distances (Lewis, 1991). Similarly, wind influences Scolytinae dispersal, influencing flight distance, and direction enabling them to cross large geographic barriers and dispersing over hundreds of kilometres (Safranyik *et al.*, 2010). These insects are frequently collected using different methods, such as window traps (type of flight interception traps) (Allison and Redak, 2017), suction traps, sticky traps, water traps, emergence traps *etc.* (Marullo *et al.*, 2021). Window traps consist of a vertical barrier that insects collide with before falling into a preservative-filled container (Bouget *et al.*, 2008) and help study insect flight height (Byers, 2011), dispersal (Ranius, 2006), activity (Jönsson *et al.*, 1986), and colonisation of new habitats like dry riverbeds (Ružanović *et al.*, 2025).

This study focused on Thysanoptera and Scolytinae ecology, habitat preferences, dispersal and spatiotemporal dynamics during the dry phase of an intermittent river. Research on these taxa in dry riverbed and riparian habitats of IRES are very scarce. Notable examples include Thysanoptera found in dry riverbeds during the long-term dry phase in Australia (Steward, 2012), Thysanoptera being a dominant taxon in experimentally rewetted gravel bars in France (Datry *et al.*, 2012); a study of a single Scolytinae species in stands of bottomland red maple along a small intermittent stream in Georgia (Nord, 1972) and extensive damage to the natural riparian forests along intermittent river in California caused by an invasive Scolytinae species (Boland, 2016). To our knowledge, no research has been conducted on Thysanoptera and Scolytinae assemblages in the Mediterranean IRES. To expand our knowledge about the use of the dry riverbed as a new habitat by pest taxa immediately after drying, this research was conducted with specific objectives: 1) to assess spatial dynamics of Thysanoptera and Scolytinae assemblages in focal IRES habitat types – dry riverbed (DRB) and riparian habitats (RH); 2) to analyse the responsiveness of these assemblages to specific environmental (different habitats – DRB and RH, and river reaches – upper reaches (UR) and lower reaches (LR) and temporal factors (different times of day – day and night); 3) to identify the impact of wind speed on Thysanoptera and Scolytinae dispersal activity.

## 2 Materials and methods

### 2.1 Study area

The study was conducted in the intermittent Dinaric karst Krčić River in the Mediterranean part of Croatia in July 2021, during its dry phase (Fig. 1). The Main Krčić Spring is a periodic spring near the foot of Dinara Mountain. The Krčić River flows for 10.5 km, ending in the Krka River at Topoljski buk waterfall (Bonacci *et al.*, 2006). Its catchment consists of Upper Triassic dolomites, Jurassic dolomites, and limestone and Quaternary alluvial deposits (Bonacci, 1985; Bonacci *et al.*, 2006). This region is characterized by a temperate humid climate with hot summers (Cfa, Köppen classification). Annual course of average, absolute minimum and maximum monthly air temperature and precipitation for the 30 yr period (1991–2020) at the nearest meteorological station town of Knin is shown in Figures S1 and S2. A climograph for 1991 to 2020 with the average monthly air temperature and precipitation is shown in Figure S3. Annual course of average air temperature and precipitation in July for the 30 yr period (1991–2020) at the nearest meteorological station town of Knin is shown in Figure S4, with average air temperature 23.8 °C and precipitation 43.4 mm. The average annual air temperature at the nearest station town of Knin in 2021 was 14.0 °C and the total annual precipitation was 1051.2 mm. In 2021, July was the warmest and the second driest (after June) month, where the average monthly air temperature at this meteorological station was 25.8 °C, the total monthly precipitation was 25.2 mm and the average monthly precipitation was 3.2 mm (Meteorological and Hydrological Service of Croatia, 2025). The Krčić River dries up nearly every year, typically from July to September, although the dry period can last until February, depending on rainfall (Bonacci, 1985).



**Fig. 1.** (a) Map showing the position of the study area in Croatia (black dot – the town of Knin, blue dot – study area); (b) sampling locations at the intermittent Krčić River (1 – upper reaches, 2 – lower reaches). Legend: SVN – Slovenia, BIH – Bosnia and Herzegovina, HUN – Hungary, DRB – dry riverbed, RH – riparian habitat.

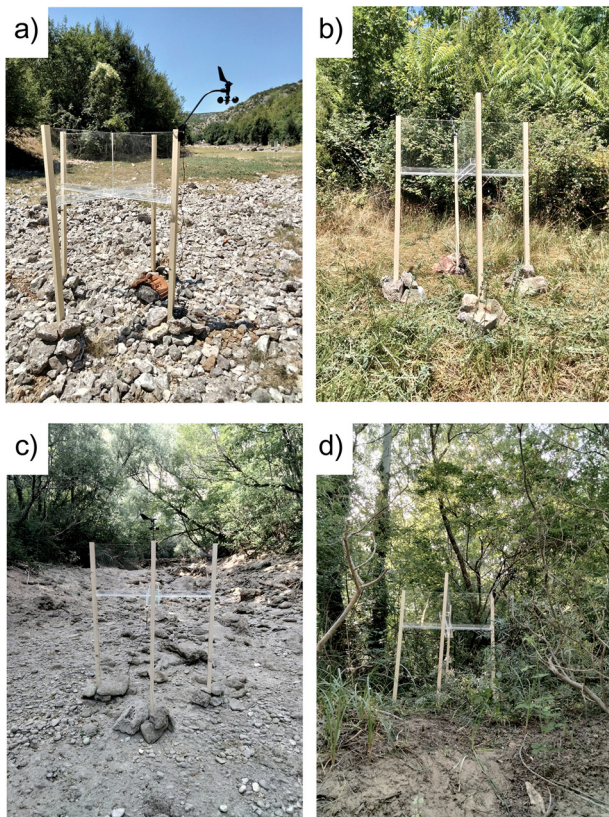
Part of the river flows on the surface, while some water seeps into the highly karstified underground as subsurface flow causing a significant water loss along the riverbed (Bonacci, 1985).

Riparian habitats along the Krčić River are characterised by different alliances of riparian vegetation in each river reach. Open grasslands predominate in the spring area, whereas dense willow shrubbery characterises the upper reaches. The lower reaches contain a weakly developed shrub layer within an old-growth poplar forest (Rebrina *et al.*, 2020). Considering the land cover, the Krčić River has low heterogeneity, with the largest percentage of surrounded area being covered by agricultural areas with significant areas of natural vegetation, then broad-leaved forest, natural grassland and finally transitional woodland/shrub with the lowest percentage (Vilenica *et al.*, 2022). The Krčić River is included in the Natura 2000 ecological network (NN 80/2019), the European Union’s largest coordinated network of protected areas. This network safeguards both terrestrial and marine areas, aiming to protect habitats and species of conservation importance. With this Mediterranean IRES, the Natura 2000 designation highlights the site's biodiversity value, protecting, among

other habitat types, aquatic habitats that support endemic taxa such as Gastropoda, *Spelaecaris*, *Monolistra*, *Niphargus*, and Odonata species (Ministry of Economy and Sustainable Development, n.d.).

## 2.2 Study design and taxa identification

Thysanoptera and Scolytinae were sampled using 12 cross-vane window traps placed in two habitats (RH and DRB) at two river reaches (UR and LR). Half of the traps were installed in the river's upper reaches (UR), while the other half were placed in its lower reaches (LR) (Fig. 2). Each window trap had eight gutters underneath four plexiglass panes, resulting in 96 gutters in total. The traps were exposed for seven days in July 2021 and were emptied every 12 h (at 7 AM and 7 PM). While flight interception traps are typically checked weekly to monitor these taxa (e.g., Aliakbarpour and Rawi, 2011), our aim was to study dispersal at a fine temporal scale rather than conduct long-term monitoring. Instead of cumulative weekly samples, we focused on shorter intervals during the critical week following riverbed drying. Though labor-intensive, this approach allowed us to capture detailed dispersal dynamics



**Fig. 2.** Examples of the study sites showing cross-vane window traps with wind speed/direction loggers along the Krčić River: (a) dry riverbed at the upper reaches; (b) riparian habitat at the upper reaches; (c) dry riverbed at the lower reaches; (d) riparian habitat at the lower reaches.

while minimizing disturbance to sensitive insect communities in protected karst habitats. Each gutter was treated as an individual sample, yielding 96 samples per sampling interval and a total of 1344 samples (96 samples  $\times$  14 intervals).

Wind speed and direction were recorded at one-minute intervals during the sampling period utilising 10 data loggers (LeWL wind logger, Logic Energy Ltd.). At each river reach, three loggers were positioned on window traps in the DRB and two in the RH, resulting in a total of six loggers in the DRB and four in the RH. After sampling, all invertebrates were preserved in 75% ethanol for subsequent analysis. Then, invertebrates were sorted to order/family level. This data was previously published in Ružanović *et al.* (2025). Thysanoptera and Scolytinae were then further identified to species level. The method of permanent preparation with a modified method was employed for Thysanoptera samples, according to Mound and Kibby (1998). In Thysanoptera specimens, sex was also determined because differences between the sexes include variations in body size, colour, wing length, number and shape of antennal segments, chaetotaxy of the head *etc.*, and may be so great that conspecific males and females may be identified as different species or even genera (Tyagi *et al.*, 2008). Collected specimens of Thysanoptera were identified to the lowest taxonomic level possible, mostly to the species, on the basis of microscopic morphological characters of adult females, using the diagnostic dichotomous keys

of Mound *et al.* (1976), Mound and Kibby (1998) and zur Strassen (2003). Scolytinae were identified according to the key of Grüne (1979).

### 2.3 Data analysis

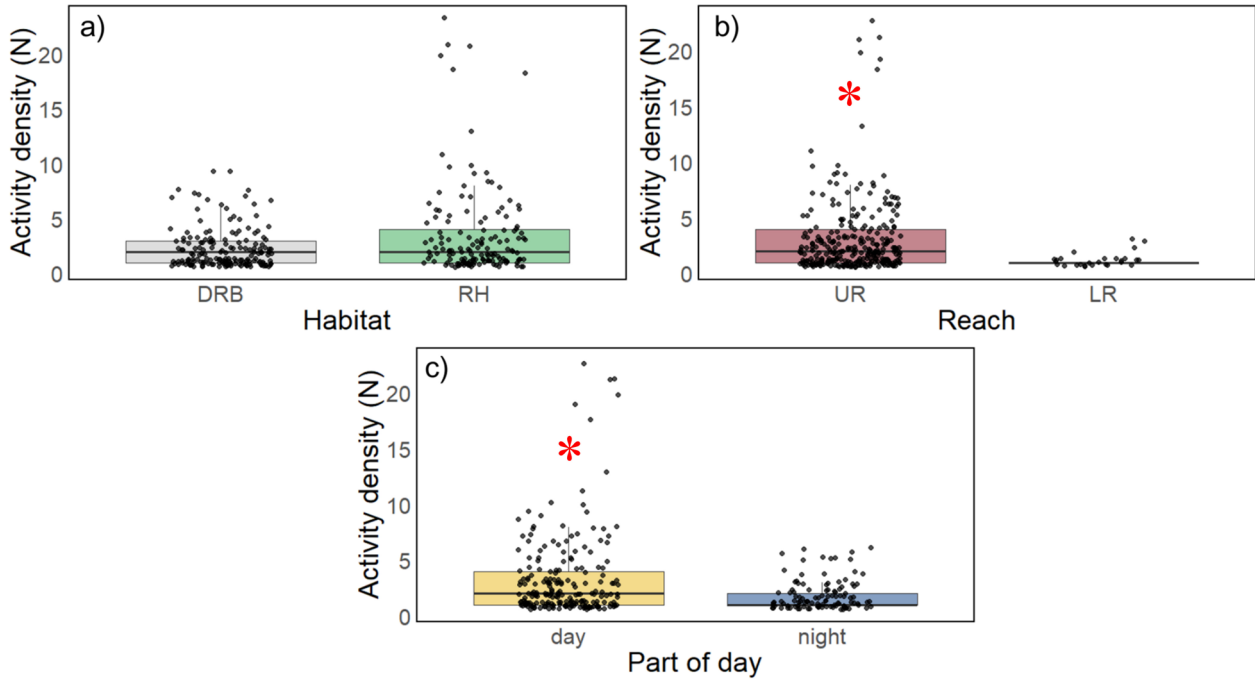
Activity density (N) was calculated independently for Thysanoptera and Scolytinae assemblages by summing the specimens collected from all cross-vane window traps deployed within each habitat type (DRB, RH), river reach (UR, LR) and time of day (day, night). Each data set was tested for normality using Shapiro–Wilk W test. Generalized linear mixed models (GLMMs) were used in R with the “glmmTMB” package (McGillicuddy *et al.*, 2025) to analyze activity density data (response variable), with habitat type, river reach, or time of day included as fixed effects, depending on the specific hypothesis. Collection events (sampling time points) were treated as repeated measures, with collection and reach included as random effects, except in cases where river reach was included as a fixed effect in the model, in which case it was not included as a random effect. To account for repeated measures within traps, a first-order autoregressive (AR(1)) structure was applied. The response variable was modelled using a negative binomial distribution with a log link function, selected after checking for overdispersion. Data were displayed as jitter boxplots with the median value, first and third quartiles, and data points (Figs. 3a-c) using the R “ggplot2” package (Wickham, 2016). Diversity could not be analysed using standard or functional diversity indices because 408 Thysanoptera individuals were destroyed during sample preparation, a step in the species identification process, leaving only abundance data without species-level resolution.

The wind speed in each habitat was averaged to 12 h intervals to align with the window trap emptying times. To characterise wind direction, prevailing winds from the south and east (45°–225°) were categorized as southeast, while non-prevailing winds from the north and west (225°–45°) were classified as northwest. The Spearman's rank correlation test was used, since normality assumptions were not met. Spearman's rank correlation coefficients were computed in R version 4.4.3 (R Core Team, 2025) to test the correlations between insect activity density and: a) average wind speed, b) average prevailing southeastern wind speeds, and c) average non-prevailing northwestern wind speeds. For plotting, we used the R “ggplot2” package functions (Wickham, 2016). Due to the very low number of Scolytinae recorded during non-prevailing northwestern winds, it was not possible to correlate their activity density with averaged non-prevailing northwestern wind speeds. To show the insect catch over time in relation to the average wind speed, data from all window traps were pooled and plotted in Tableau 2021.1. (Tableau, 2022).

## 3 Results

### 3.1 Thysanoptera activity density and taxonomic composition

A total of 914 Thysanoptera individuals were collected, and while abundance data is available for the whole sampling period, due to equipment failure during the preparation for species identification, 408 out of 914 individuals were lost and



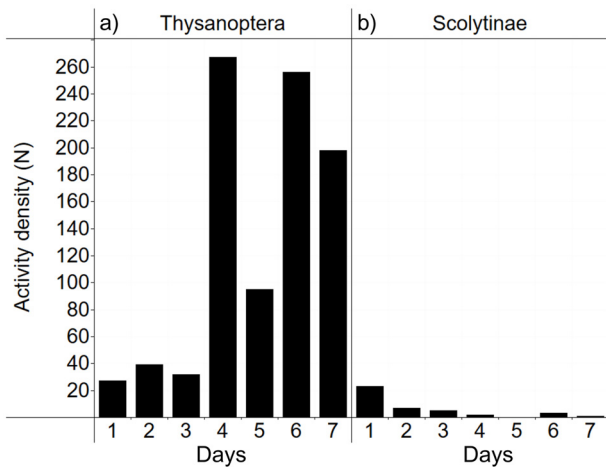
**Fig. 3.** Activity density (N) of Thysanoptera: (a) in dry riverbed (DRB) and riparian (RH) habitat; (b) in upper reaches (UR) and lower reaches (LR); (c) during the day and night at the Krčić River area. Boxplots show the median value, first and third quartiles, and data points.

**Table 1.** Results of generalized linear mixed models testing the effects of habitat (DRB = Dry riverbed, RH = Riparian habitat), time of day, and river reach (UR = Upper reach, LR = Lower reach) on Thysanoptera activity density. Estimates represent effect sizes, with positive values indicating higher activity density in the second category of each comparison. Statistically significant results ( $p < 0.05$ ) are shown in bold. “Dominant” indicates the category with higher activity density when significant.

Thysanoptera		Estimate RH/Night/UR	Z value	P value	Dominant
Habitat differences (DRB vs. RH)	Whole data	-0.386	-0.99	0.320	N/A
	Upper reach	0.258	1.21	0.230	N/A
	Lower reach	<b>-1.917</b>	<b>-3.10</b>	<b>0.002</b>	<b>DRB</b>
	Day	0.141	0.69	0.490	N/A
	Night	-0.704	-1.04	0.300	N/A
Time of day differences (Day vs. night)	Whole data	<b>-1.252</b>	<b>-2.23</b>	<b>0.026</b>	<b>Day</b>
	Upper reach	<b>-1.391</b>	<b>-2.53</b>	<b>0.012</b>	<b>Day</b>
	Lower reach	-0.647	-1.02	0.310	N/A
	Dry riverbed	-0.906	-1.51	0.130	N/A
	Riparian habitat	<b>-1.605</b>	<b>-2.77</b>	<b>0.006</b>	<b>Day</b>
Reach differences (UR vs. LR)	Whole data	<b>3.227</b>	<b>10.08</b>	<b>&lt;0.001</b>	<b>UR</b>
	Dry riverbed	<b>2.384</b>	<b>7.11</b>	<b>&lt;0.001</b>	<b>UR</b>
	Riparian habitat	<b>4.863</b>	<b>8.38</b>	<b>&lt;0.001</b>	<b>UR</b>
	Day	<b>3.480</b>	<b>12.40</b>	<b>&lt;0.001</b>	<b>UR</b>
	Night	<b>3.260</b>	<b>4.49</b>	<b>&lt;0.001</b>	<b>UR</b>

could not be processed further than the abundance data. Thysanoptera activity density did not differ significantly between habitats when considering the full dataset (Tab 1), the upper reach, or during either the day or night. However, in the lower reach, activity density was significantly higher in the dry riverbed compared to the riparian habitat ( $p = 0.002$ ).

Comparisons between day and night revealed significantly higher activity density during the day across the whole dataset ( $p = 0.026$ ). This pattern was also evident in the upper reach ( $p = 0.012$ ) and within the riparian habitat ( $p = 0.006$ ). No significant day–night differences were found in the lower reach or in the dry riverbed. Reach-level differences were observed,



**Fig. 4.** Activity density (N) of (a) Thysanoptera and (b) Scolytinae over the period of seven days (each day represents 24-h sampling interval) at the Krčić River area.

with significantly higher activity density in the upper reach compared to the lower reach across all data ( $p < 0.001$ ). This pattern was present in both habitat types: dry riverbed ( $p < 0.001$ ) and riparian ( $p < 0.001$ ), and during both the day ( $p < 0.001$ ) and night ( $p < 0.001$ ; Tab. 1).

Among the examined specimens, 484 were identified to the species level, eight to the genus level, and 14 could not be identified due to missing body parts essential for identification. The identified individuals belonged to 31 different taxa (Tab. S1). The most abundant taxon was *Thrips tabaci* Lindeman, 1889 with a total of 135 individuals, followed by *Thrips vulgatissimus* Haliday, 1836 ( $N=103$ ), *Thrips viminalis* Uzel, 1895 ( $N=54$ ), *Thrips trehernei* Priesner, 1927 ( $N=47$ ) and *Thrips meridionalis* (Priesner, 1926) ( $N=29$ ), while some of the rare taxa included *Frankliniella occidentalis* (Pergande, 1895), *Thrips mancosetosus* Priesner, 1964 and *Thrips pini* (Uzel, 1895) ( $N=1$ ). The majority of examined specimens were females (92%), while males (6%) were far less abundant. The sex of 10 individuals could not be determined due to damaged abdominal segments bearing genitalia (Tab. S1). Taxa richness was higher at the DRB compared to the RH when analysing both river reaches together (Tab. S1), with the most numerous taxa (mentioned above) mostly found in the RH, and in smaller numbers in the DRB. The exception was *T. meridionalis* which was more abundant in the DRB (Tab. S1). Taxa richness was higher at the UR comparing to the LR when analysing both habitats together (Tab. 1) and also higher during the day than at night (Tab. 1). At the beginning of the experiment (day 1), the number of individuals was low, then suddenly increased in the second half of the experiment (day 4) and finally dropped on the last day of the study (day 7) (Fig. 4a).

### 3.2 Scolytinae activity density and taxonomic composition

We collected a total of 39 Scolytinae individuals. Their activity density was significantly higher in the riparian habitat compared to the dry riverbed when considering the full dataset ( $p=0.005$ ; Tab. 2), and this pattern was also present in the

upper reach ( $p=0.040$ ). In the lower reach, however, the difference between habitats was not significant, nor were differences detected during the day or night. Comparisons between day and night did not reveal any significant differences in activity density, either across the full dataset or the upper reach, lower reach, dry riverbed, or riparian habitat. No significant differences in activity density were observed between the upper and lower reaches in the full dataset, in the dry riverbed, or in the riparian habitat. Likewise, reach-level comparisons showed no significant differences during the day, or night.

Out of 39 individuals in total, 37 individuals were identified to the species level, while two could not be identified due to missing body parts essential for identification. A total of three species were found, of which the most abundant was *Xyleborus saxeseni* (Ratzeburg, 1837) ( $N=30$ ), which was mostly found in the RH, and in smaller numbers in the DRB (Tab. S2). Taxa richness was higher in the RH than in the DRB and also at the UR than at the LR (Tab. S2). More species were recorded during the night than during the day (Tab. S2). The number of Scolytinae individuals varied during the window traps exposure period. At the beginning of the experiment (day 1), an increase in the number of individuals was recorded, after which the number decreased sharply (days 4–7) (Fig. 4b).

### 3.3 Effect of wind speed and direction on Thysanoptera and Scolytinae

Thysanoptera activity density was positively correlated with averaged wind speed (Spearman's correlation,  $\rho=0.38$ ,  $p < 0.001$ ; Fig. 5a) and averaged prevailing southeastern wind speed ( $\rho=0.43$ ,  $p < 0.001$ ; Fig. 5b), while no correlation was recorded with the averaged non-prevailing northwestern wind speed ( $\rho=0.34$ ,  $p=0.31$ ; Fig. 5c). The activity density varied over time depending on period and wind speed. Towards the end of the experiment, it followed the wind speed pattern (Fig. 6a).

Scolytinae activity density was not correlated with averaged wind speed ( $\rho=-0.25$ ,  $p=0.22$ ) nor with averaged prevailing southeastern wind speeds ( $\rho=-0.24$ ,  $p=0.26$ ). Their activity density did not follow the wind speed pattern (Fig. 6b).

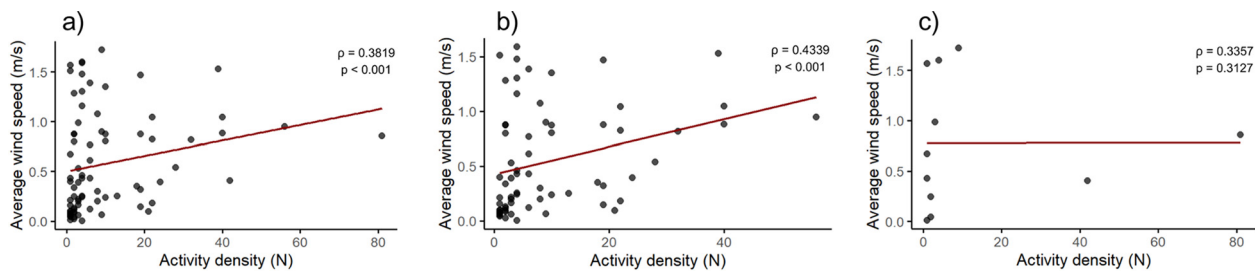
## 4 Discussion

### 4.1 Thysanoptera prefer open sunny upper reaches and use dry riverbed as a corridor

In our study, more Thysanoptera taxa were found in the dry riverbed than in the riparian habitat, likely due to several single-individual species found only at the upper reach of the DRB. *A. intermedius* and *T. mancosetosus* were found only at the DRB in the UR, reflecting their preference for open habitats (Kucharczyk, 2010; Gruss *et al.*, 2019), like those of the Krčić River upper reach. Dendrophilous species, *D. degeeri* could have flown to the DRB from the *Fraxinus ornus* L. trees found in adjacent upland habitats (Rebrina *et al.*, 2020), as this species is known to feed on its leaves (Kucharczyk *et al.*, 2025). Although *T. pini* typically inhabits coniferous trees (Kucharczyk, 2010; Masarovič *et al.*, 2022), recent findings

**Table 2.** Results of generalized linear mixed models testing the effects of habitat (DRB = Dry riverbed, RH = Riparian habitat), time of day, and river reach (UR = Upper reach, LR = Lower reach) on Scolytinae activity density. Estimates represent effect sizes, with positive values indicating higher activity density in the second category of each comparison. Statistically significant results ( $p < 0.05$ ) are shown in bold. “Dominant” indicates the category with higher activity density when significant.

Scolytinae		Estimate RH/Night/UR	Z value	P value	Dominant
Habitat differences (DRB vs. RH)	Whole data	<b>1.094</b>	<b>2.81</b>	<b>0.005</b>	<b>RH</b>
	Upper reach	<b>1.483</b>	<b>2.06</b>	<b>0.040</b>	<b>RH</b>
	Lower reach	0.908	1.78	0.076	N/A
	Day	1.013	1.84	0.067	N/A
	Night	1.105	1.94	0.053	N/A
Time of day differences (Day vs. night)	Whole data	-0.751	-0.10	0.925	N/A
	Upper reach	0.503	0.71	0.475	N/A
	Lower reach	-0.408	-0.47	0.642	N/A
	Dry riverbed	-2.09e-06	0.00	1.000	N/A
	Riparian habitat	9.48e-05	0.00	0.999	N/A
Reach differences (UR vs. LR)	Whole data	-0.306	-0.69	0.493	N/A
	Dry riverbed	-0.707	-0.74	0.461	N/A
	Riparian habitat	-0.097	-0.22	0.826	N/A
	Day	-0.789	-1.42	0.160	N/A
	Night	0.141	N/A	N/A	N/A

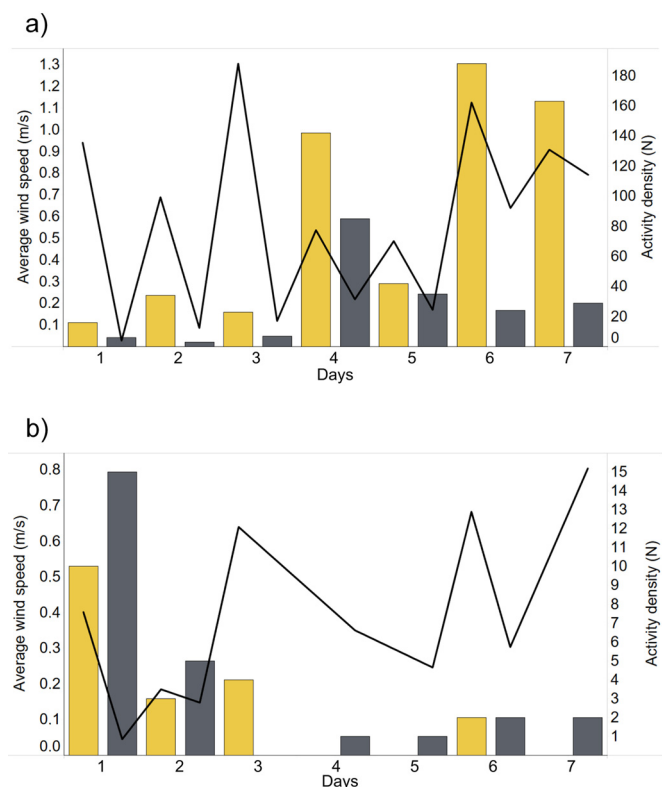


**Fig. 5.** Spearman rank correlation between activity densities of Thysanoptera (N) and wind speed: (a) average and (b) average prevailing south-easterly and (c) average non-prevailing north-westerly winds.

in open habitats (Masarovič *et al.*, 2022) may explain its record in the DRB at the UR. It likely originates from *Pinus nigra* J. F. Arnold trees recently planted upstream, and may be using DRB as a migration corridor because it offers easier movement compared to denser riparian vegetation. Aerial movement along the DRB of the Krčić River is an important dispersal mechanism for Thysanoptera, as indicated by high activity density and species richness in this habitat, even early in the dry phase (The Krčić River dries up typically from July to September). More species and individuals are likely to use the DRB as the dry period progresses. They may prefer DRB over RH as a dispersal corridor, as the open airspace facilitates flight, whereas vegetation in the RH can be perceived as a physical barrier for certain open habitat species. Moreover, at the beginning of the dry phase, predator abundance in the DRB is likely lower, since Heteropterans, ladybugs and web-spinning spiders, which prey on Thysanoptera, are mostly found on vegetation (Sabelis and Van Rijn, 1997; Montserrat *et al.*, 2000; Kundoo and Khan, 2017). This reduced predation may further encourage Thysanoptera to use the DRB as a dispersal corridor.

Significantly higher Thysanoptera activity density and higher taxa richness at UR compared to the LR could be related to the differences in habitat characteristics and temperature between reaches. Higher air temperatures positively influence Thysanoptera activity, abundance, and population growth rate (Morsello *et al.*, 2008), with peak population densities typically observed in hotter months (Kumar *et al.*, 2014). Both dry riverbed and riparian habitat at the UR have sparser vegetation and greater exposure than the more densely vegetated LR resulting in higher air temperatures (Rebrina *et al.*, 2020; Rebrina *et al.*, *in preparation*). Such conditions could change in the future due to the fast-spreading of the resistant invasive tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle) (Motti *et al.*, 2021) in the UR. If unmanaged, this species could dominate, change plant community composition and shift the habitat from open to possibly closed canopy, negatively impacting open-habitat species.

The high abundance of *T. tabaci*, the dominant Tysanoptera species in our study, suggests its peak activity in July, aligning with previous findings of population peaks between June and



**Fig. 6.** Window trap catch of (a) Thysanoptera and (b) Scolytinae at 12-h intervals (day, 7 AM–7 PM in yellow; night, 7 PM–7 AM in grey) in both habitats over the period of seven days. The black line represents the average wind speed at each sampling time.

August (Bergant *et al.*, 2005). Although *T. tabaci* prefers hot and dry habitats (Mound, 1997) in our study it was more abundant in the RH. Despite generally higher humidity, riparian habitats in Mediterranean karst rivers can become hot and dry in summer (Gasith and Resh, 1999), creating favourable conditions. Combined with greater food availability and shelter provided by the riparian vegetation, these factors likely support higher *T. tabaci* activity density in the RH. The higher Thysanoptera activity density during the day was also largely driven by *T. tabaci*, consistent with Smith *et al.* (2016), who noted its activity during the day, mostly before dusk. This aligns with its needs for higher temperatures and solar radiation for their optimal flight (Kumar *et al.*, 2014) and can explain the higher Thysanoptera activity density in the more open UR with high light intensity, compared to the forested LR. Given the temperature sensitivity of Thysanoptera assemblages, including the dominant *T. tabaci*, climate change will likely affect their abundances. Predictions already suggest more *T. tabaci* generations per season (Bergant *et al.*, 2005) which will increase its spread and potential impact on new habitats.

#### 4.2 Scolytinae favour shaded riparian habitats of the lower reaches

*Xyleborus saxesenii* was the most abundant Scolytinae in our study, aligning with its typical emergence (flying out from galleries in wood or bark of host trees) in July and August (Saruhan and Akyol, 2013). Although riparian habitats in our study were relatively dry and hot, they were still more humid

and cooler than the harsher dry riverbeds. This likely explains the species' preference for the less extreme and more densely vegetated riparian habitat. Environmental factors, especially temperature, highly affect Scolytinae presence and flight activity. For *X. saxesenii*, optimal flight occurs between 10 °C and 32 °C, with a preference for afternoon activity (Hosking, 1973; Pernek *et al.*, 2006). In our study, it was likely active in the late afternoon and, avoiding heat, entered night collecting period, after 7 PM. Night temperatures remained above 14.5 °C (Rebrina *et al.*, *in preparation*), well above the lower threshold for flight. As a xylomycetophagous species feeding on mutualistic ambrosia fungi and wood, *X. saxesenii* depends on humid conditions crucial for fungal growth (Biedermann *et al.*, 2013). Since droughts become more frequent in Mediterranean rivers (Skoulikidis *et al.*, 2017), desiccation threatens fungal mutualists (Biedermann *et al.*, 2013), which can negatively impact Scolytinae assemblages. In our study, this species was found in both river reaches, showing longitudinal dispersal, possibly also allowing the dispersion of fungi into new habitats. The individuals found in the DRB were likely in flight between the opposite riparian habitats.

#### 4.3 Constant light winds aid Thysanoptera dispersal but have no effect on Scolytinae

In our study, the average wind speed fell within the “light air” category according to the Beaufort Scale (WMO, 1970), conditions under which Thysanoptera showed peak activity. This aligns with previous findings showing that *T. tabaci*, our most dominant species, prefers continuous and weak winds for dispersal (Smith *et al.*, 2016). Though weak flyers, their fringed wings allow long-distance dispersal enhanced by wind (Lewis, 1991; Smith *et al.*, 2015). Macropterous Thysanoptera can produce mass flights in suitable weather (Lewis, 1964), as seen in the latter part of our sampling period, while micropterous or wingless individuals can be carried passively by wind (Lewis, 1964) contributing to aerial plankton (Ptatscheck *et al.*, 2018). The significant correlation between Thysanoptera activity density and average prevailing wind direction further suggests their dependence on predominant winds, consistent with previous studies (Jokar and Mohammadnia, 2024).

Our study found no correlation between Scolytinae activity density and wind speed, despite evidence that wind can influence their flight (Jones *et al.*, 2019). This may result from low population densities in these habitats and the time of sampling, when *X. saxesenii*, the most abundant species in our study, is less active compared to spring (Robinson-Baker, 2024). Scolytinae, such as *X. saxesenii*, do not fly out immediately after reaching adulthood but rather delay their dispersal due to unfavourable environmental conditions (Kirkendall *et al.*, 2015). While they can disperse via wind to find new hosts for reproduction (Jones *et al.*, 2019), dispersal may not occur every generation if the same host is recolonized (Raffa *et al.*, 2015).

#### 4.4 Thysanoptera can be pests, pollinators, virus carriers and facultative predators

Although Thysanoptera are often regarded as major agricultural pests, only 1% are considered harmful to crops (Pizzol *et al.*, 2017). In our study, we identified direct pests

such as *Thrips major* Uzel, 1895 and *T. meridionalis* (Gallardo-Ferrand *et al.*, 2024). Furthermore, recorded species such as *T. tabaci*, *Frankliniella intonsa* (Trybom, 1895) and *F. occidentalis*, can indirectly threaten plants as vectors of tomato spotted wilt tospovirus (TSWV) (Raspudić, 2016), which damages plant leaves and fruits (Jones, 2005). Their ability to spread TSWV through aerial transport poses a potential risk to nearby agricultural areas. Some species recorded in our study were recently recognized for having important ecological roles, especially as effective pollinators (Mound, 2005), such as *A. intermedius*, *F. intonsa*, *F. occidentalis*, and *T. tabaci* (Kirk, 1984). Moreover, *Scolothrips* Hinds, 1902 species can serve as beneficial biological control agents against leaf-feeding mites (Mound, 2011).

The most abundant species in our study, *T. tabaci*, is a cosmopolitan, phytophagous pest (especially on onion and tobacco), and a facultative predator feeding on various arthropods (Mound, 2005). It is widespread in Croatia (Raspudić and Ivezić, 1998; Raspudić *et al.*, 2009), occurring in Dalmatian citrus plantations (Šimala *et al.*, 2017), vegetables and ornamental plants (Šimala *et al.*, 2023). Recorded on 29 plant families in Croatia, it is most common on Asteraceae, Fabaceae, Rosaceae and Poaceae (Raspudić and Ivezić, 1998), all of which were present in at least one habitat in our study. We found that males accounted for only 6% of total Thysanoptera catch, reflecting the species' usual parthenogenetic reproduction, with males being common only in the presumed area of origin (Mound, 1977).

#### 4.5 New Thysanoptera records for Croatia

Out of 28 species identified in this study, 21 have already been reported from Croatia and represent 17.65% of the last published Thysanoptera check-list for Croatia (Raspudić *et al.*, 2003). In this study we recorded 4.88% of European Thysanoptera fauna (Collins, 2010). A total of 119 species is listed in the Croatia's Thysanoptera check-list (Raspudić *et al.*, 2003), while a certain number of new species in Croatia were subsequently found (Šimala and Masten Milek, 2008; Raspudić *et al.*, 2009; Šimala *et al.*, 2017, 2019, 2023). With this research, we documented seven new species for Croatian fauna: *Thrips conferticornis* Priesner, 1922, *Thrips dubius* Priesner, 1927, *Thrips inopinatus* zur Strassen, 1963, *T. mancosetosus*, *T. pini*, *Thrips verbasci* (Priesner, 1920) and *T. viminalis*. Thus, this research has contributed to the increase in the number of Thysanoptera species already known in Croatia, elucidating our understanding of their regional but also European distribution.

#### 4.6 Drought and rising temperatures might impact Scolytinae populations in the Krčić River

In Croatia, the research of Scolytinae has been focused on presence of rare (Lukić *et al.*, 2019) or invasive species (Pernek *et al.*, 2025), forest pest outbreaks (Hrašovec *et al.*, 2008; Pernek *et al.*, 2019), control methods (Pernek *et al.*, 2006), parasites and pathogens (Maksimović, 1979; Pernek *et al.*, 2009), and Scolytinae overwintering strategy (Kasumović *et al.*, 2019). The most abundant species recorded in the Krčić River, *X. saxesenii*, is a well-known xylophagous

beetle in Croatia which targets oak trees in mid-spring (Hrašovec *et al.*, 2005; Franjević *et al.*, 2019). Frequent droughts and rising temperatures weaken trees, and together with anthropogenic activities such as deforestation and inadequate harvesting procedures, enable Scolytinae population growth (Hrašovec *et al.*, 2008; Battisti and Larsson, 2015) and may lead to outbreaks, which was already recorded in Croatia (Hrašovec *et al.*, 2005; Pandžić *et al.*, 2022). Such outbreaks cause significant timber damage and subsequent economic losses (Pernek *et al.*, 2009). While Krčić River has not yet faced significant anthropogenic modifications, as an intermittent river in Mediterranean, it is vulnerable to prolonged droughts, rising temperature and landscape changes (Skoulikidis *et al.*, 2017; Mimeau *et al.*, 2025) that could also impact Scolytinae populations and have higher negative ecological consequences on riparian plant and animal communities.

## 5 Conclusions

This study provides new insights into the ecology of Thysanoptera and Scolytinae assemblages in the karst Mediterranean intermittent river with an emphasis on the importance of dry riverbeds as longitudinal dispersal corridors for pest taxa. As dry phases become longer with climate change, such corridors may increasingly support the spread of various taxa along the entire river course. Due to their roles as agricultural and forest pests, vectors of plant viruses, but also as important pollinators, future studies on Thysanoptera and Scolytinae habitat requirements and population densities are highly recommended. Climate change can accelerate their life cycles, resulting in increased number of generations and population densities which could negatively impact sensitive and biodiverse riparian vegetation. Since these taxa are already included in agricultural and forest monitoring and management programs, we recommend also incorporating them into intermittent Mediterranean river monitoring as systematic research and regular monitoring are crucial for conserving riparian vegetation and preserving biodiversity of intermittent rivers.

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#### Conflicts of interest

The authors declare no competing interests.

## Data availability statement

Data are available from the authors upon reasonable request.

## Author contribution statement

Conceptualisation: Andreja Brigić; Developing methods: Andreja Brigić; Conducting the research: Andreja Brigić, Lea Ružanović, Fran Rebrina, Marina Vilenica; Data analysis: Zuzana Redžović, Lea Ružanović, Mladen Šimala, Boris Hrašovec, Fran Rebrina, Andreja Brigić; Data interpretation: Zuzana Redžović, Lea Ružanović, Fran Rebrina, Andreja Brigić; Preparation of figures and tables: Lea Ružanović, Zuzana Redžović; Writing: Zuzana Redžović, Lea Ružanović, Fran Rebrina, Mladen Šimala, Boris Hrašovec, Marina Vilenica, Andreja Brigić.

## Supplementary material

**Table S1.** Thysanoptera taxa and their activity density (N) in various habitats (RH - riparian habitat, DRB - dry riverbed), river reaches (UR - upper reaches, LR - lower reaches), times of day (day, night) and sex ratio (male, female) in the intermittent Krčić River, Croatia.

**Table S2.** Scolytinae taxa and their activity density (N) in various habitats (RH - riparian habitat, DRB - dry riverbed), river reaches (UR - upper reaches, LR - lower reaches) and times of day (day, night) in the intermittent Krčić River, Croatia.

**Figure S1.** Average, absolute minimum, and absolute maximum monthly temperatures from 1991 to 2020, measured at the Knin meteorological station (closest to Krčić). Data provided by the Croatian Meteorological and Hydrological Service (DHMZ). Temperatures are shown in degrees Celsius (°C).

**Figure S2.** Average, absolute minimum, and absolute maximum monthly precipitation from 1991 to 2020, measured at the Knin meteorological station (closest to Krčić). Data provided by the Croatian Meteorological and Hydrological Service (DHMZ). Precipitation is shown in millimeters (mm).

**Figure S3.** Average monthly temperature and precipitation from 1991 to 2020 at the Knin meteorological station. Data provided by the Croatian Meteorological and Hydrological Service (DHMZ). Temperature is shown in degrees Celsius (°C), and precipitation in millimeters (mm).

**Figure S4.** Average temperature and precipitation in the month of July (sampling period) for each year from 1991 to 2020, measured at the Knin meteorological station. Data provided by the Croatian Meteorological and Hydrological Service (DHMZ). Temperature is shown in degrees Celsius (°C), and precipitation in millimeters (mm).

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2025025/olm>.

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