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The diet spectrum of *Pelophylax* waterfrogs from mainland Greece, including novel data for the Epirus Waterfrog, *Pelophylax epeiroticus* (Schneider et al., 1984)

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Understanding the trophic ecology of amphibians is essential for interpreting their role in freshwater ecosystems and their responses to spatial and environmental heterogeneity (Keller et al., 2009; Hocking and Babbit, 2014; Huckembeck et al., 2018). Diet composition reflects both individual-level foraging behaviour and species-level niche breadth, which may vary across species, regions, and local habitats due to environmental constraints or prey availability (Le et al., 2018; Lunghi et al., 2020; De Toledo Moroti, 2021).

Water frogs of the genus *Pelophylax* are generally considered opportunistic predators, typically feeding on a wide range of aquatic and terrestrial invertebrates (Karaica et al., 2016; Plitsi et al., 2016; Pesarakloo et al., 2017; Pafilis et al., 2019), and occasionally also on vertebrates (e.g., Országhová et al., 2003; Baier et al., 2009; Nicolaou et al., 2014; Katsiyiannis and Tzoras, 2020; Khashab and Jablonski, 2025), including other amphibians (Pille et al., 2022). Although this generalist foraging strategy is well documented, relatively few studies have systematically assessed dietary composition in endemic species or how this composition varies among closely related species (Mollov, 2008; Karaica et al., 2016; Plitsi et al., 2016; Pesarakloo et al., 2017; Breka et al., 2024).

Similarly, knowledge of the trophic ecology of Balkan waterfrogs remains rather fragmentary (e.g., Plötner, 2025). While several studies have addressed diet composition in widespread taxa in the Balkans (e.g., Karaica et al., 2016, Plitsi et al., 2016), nothing is known about the feeding ecology of the endemic Epirus Waterfrog, *P. epeiroticus* (Schneider et al., 1984). This species has a relatively small range, restricted to northwestern Greece and southern Albania (Papežík et al., 2023). Despite its conservation relevance, ecological information beyond basic distributional data is largely lacking (Sofianidou and Schneider, 1989).

The taxonomic status of *P. epeiroticus* is unambiguous, whereas that of *P. kurtmuelleri* remains controversial. Populations from the southwestern Balkans (including Greece) have been variously classified as belonging either to this species (e.g., Plötner et al., 2025), to *P. ridibundus* (Speybroeck et al., 2010, 2020), or to the recently recognised subspecies *P. ridibundus kurtmuelleri* (Dufresnes et al., 2024; Frost, 2024). The taxa *P. ridibundus* and *P. kurtmuelleri* can be distinguished only genetically [e.g., using markers such as mitochondrial *ND2* (Papežík et al. 2023) or several nuclear markers (Dufresnes et al., 2024)], but not morphologically (Papežík et al., 2021). Moreover, both taxa appear to form an extensive hybrid zone in northeastern Greece, the region from which the biological material for our study was collected. Given the controversial taxonomic status of the populations inhabiting the study area and the hybridisation between them, we did not distinguish between *P. r. ridibundus* and *P. r. kurtmuelleri*, and refer to them collectively as *P. ridibundus/P. kurtmuelleri*.

In this study, we examined the diet composition of waterfrog species (*P. epeiroticus* and *P. ridibundus/P. kurtmuelleri*) across multiple localities in western and northeastern mainland Greece. Using presence/absence stomach content data, we aimed to identify the scale and structure of trophic niche variation in *Pelophylax* frogs and to evaluate the relative contributions of species identity and spatial factors to dietary composition.

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Materials and Methods

Specimen collection. Data were collected in western Greece in July 2021 and in northeastern Greece in July 2023 (Fig. 1, Table 1). A total of 89 individuals of water frogs were captured. During each field session, parasitological dissections were performed, and stomach contents were preserved in 96% ethanol.

Frogs were assigned to species based on morphological characteristics and the mitochondrial *ND2* gene (Papežík et al., 2021, 2023; Strachinis et al., 2025). All individuals were processed and analysed from a biomolecular perspective following the protocol described in Papežík et al. (2023).

Data analyses. Stomach contents of frogs were identified to the lowest feasible taxonomic level using standard identification keys (Ionescu and Lăcătuşu, 1971; Dierl, 1978; Crişan and Mureşan, 1999) and a Leica EZ4 stereomicroscope. When a lower taxonomic level was specified, individuals belonging to that category were excluded from the corresponding higher-level category. Because the number of prey items could not be reliably estimated, particularly when multiple undifferentiated residues were present, the data were converted into a presence/absence matrix. Frogs with empty stomachs, as well as plant remains accidentally ingested with food, were excluded from the analyses. In total, 59 individuals were retained for analysis. The majority of analyses were performed using the *vegan* package (Oksanen et al., 2025) in the R statistical environment, v. 4.1.3 (R Core Team, 2022).

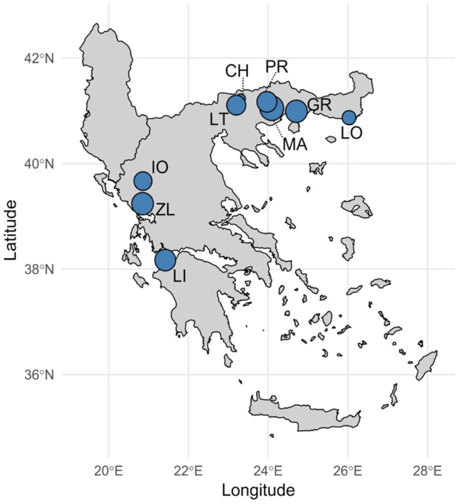

Figure 1. Sampling localities of *Pelophylax* water frogs in Greece involved in the diet spectrum analysis. Circle sizes are proportional to the number of sampled individuals per locality. Locality abbreviations are listed in Table 1.

The proportional occurrence of each prey taxon was calculated across all samples to describe the relative contribution of individual prey types. Prey richness was calculated at both the individual level (number of prey taxa per individual) and the dataset level (total number of unique prey taxa recorded).

Using the R *betapart* package (Baselga and Orme, 2012), we computed total beta diversity (β_{JAC}) and partitioned it into two additive components: species turnover (β_{JTU}) and nestedness-resultant dissimilarity (β_{JNE}). The Jaccard index was used as the dissimilarity metric. Species turnover (β_{JTU}) quantifies taxon replacement between samples, while nestedness-resultant dissimilarity (β_{JNE}) reflects differences in richness when one sample represents a subset of

Table 1. List of sampled localities, abbreviations used in the text, regional classification, geographic coordinates, and sample sizes. EPE column indicate number of sampled *P. epeiroticus*, RID/KURT number of sampled *P. ridibundus*/*P. kurtmuelleri*.

Locality	Abbreviation	Region	Latitude	Longitude	N of Individuals	EPE	RID/KURT
Gravouna	GR	Northeastern Greece	41.00	24.67	9	0	9
Cheimaros	CH	Northeastern Greece	41.12	23.25	1	0	1
Lithopos	LT	Northeastern Greece	41.14	23.22	6	0	6
Loutros	LO	Northeastern Greece	40.87	26.03	2	0	2
Mavrolefki	MA	Northeastern Greece	41.05	24.09	12	0	12
Prosotsani	PR	Northeastern Greece	41.17	23.97	7	0	7
Ioannina	IO	Western Greece	39.69	20.86	5	3	2
Limanaki	LI	Western Greece	38.17	21.42	8	8	0
Zirou lake	ZL	Western Greece	39.24	20.85	9	2	7

another. This decomposition allows distinguishing whether dissimilarity among individuals was driven primarily by prey replacement or by differences in prey richness and subset composition. Additionally, sampling completeness was evaluated using species accumulation curves generated with random permutations, providing estimates of cumulative prey richness as a function of sample size. Accumulation curves were estimated using *specaccum()* function.

Diet composition was assessed using non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity. The analysis was performed in two dimensions ($k = 2$) with 100 random starts (trymax = 100), and the final stress value was used to evaluate the goodness-of-fit.

Due to limited ecological data for *P. epeiroticus*, relative contribution, individual prey richness, and the accumulation curve were also calculated for the dataset containing only individuals of *P. epeiroticus* ($n = 13$).

All visualisations were created using the R *ggplot2* package (Wickham, 2016).

Results and Discussion

Overall prey composition. Across all individuals, 26 prey taxa were identified. The most frequently recorded groups included Araneae (40.7% of all recorded prey), Coleoptera (39%), and Formicidae (27.1%) (Fig. 2A). Several additional arthropod taxa, such as Orthoptera, Grylloidea, and Diptera (approximately 17%), were also commonly observed, while the remainder of prey types occurred less frequently.

Partitioning of total beta diversity based on Jaccard dissimilarity indicated that dietary variation among individuals was driven almost exclusively by species turnover ($\beta_{JTU} = 0.971$), with a negligible contribution of nestedness ($\beta_{JNE} = 0.011$). This suggests that individual frogs consumed largely distinct sets of prey, rather than differing in richness or completeness of a shared prey pool.

Individual dietary richness ranged from one to seven prey taxa per frog, with most individuals containing between one and three distinct prey types (Fig. 2B). The species accumulation curve showed a gradual increase without reaching a clear asymptote (Fig. 2C), suggesting that additional sampling might further increase observed diversity.

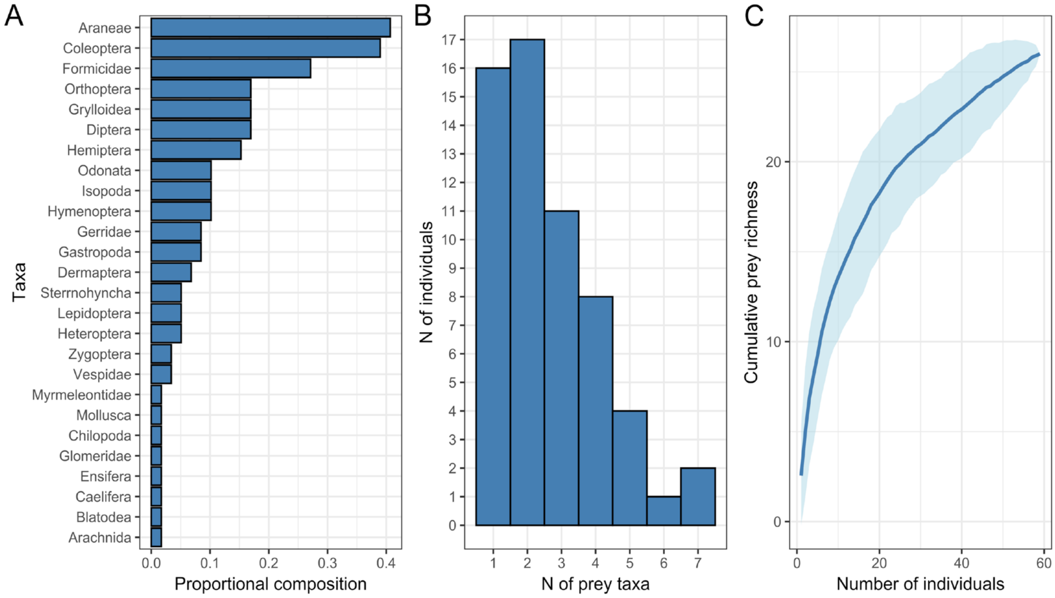

Figure 2. Summary of prey diversity detected in the stomach contents of all sampled *Pelophylax* individuals ($n = 59$). (A) Proportional composition of prey taxa across all individuals. (B) Distribution of individual prey richness, expressed as the number of distinct prey taxa per individual. (C) Species accumulation curve showing cumulative prey richness as a function of the number of sampled individuals. The shaded area represents the 95% confidence interval.

Pelophylax epeiroticus. When analysing only *P. epeiroticus* (*n* = 13), a total of 13 prey taxa were identified. The most frequently encountered groups in this subset were Formicidae and Araneae (both 18.2%), followed by Grylloidea and Diptera (both 13.6%) (Fig. 3A). Most individuals consumed one or two prey types (Fig. 3B), and the accumulation curve did not reach a plateau, indicating incomplete prey detection within the available sample (Fig. 3C).

Pelophylax ridibundus/P. kurtmuelleri. In *P. ridibundus*/*P. kurtmuelleri* (*n* = 46), dietary analysis revealed the presence of 26 distinct prey taxa. The most frequently recorded groups were Coleoptera (56.8%) and Araneae (54.1%), followed by Formicidae (32.4%) (Fig. 4A). The majority of individuals consumed one to three distinct prey types (Fig. 4B). The species accumulation curve showed no clear asymptote, suggesting that prey diversity was not fully captured within the current sampling effort (Fig. 4C).

Non-metric multidimensional scaling (NMDS). An NMDS ordination of stomach content data revealed moderate dietary variation among individuals, with a final stress value of 0.104 (Fig. 5). Most samples were distributed near the centre of the ordination space, although some individuals showed more distinct prey compositions. Prey taxa were broadly scattered throughout the ordination space, with no obvious clustering structure.

Our study revealed that water frogs of the genus *Pelophylax* in mainland Greece exhibit predominantly opportunistic feeding strategies, with diets composed mainly of diverse arthropod groups such as Araneae, Coleoptera, and Formicidae. Despite the taxonomic differences between *P. epeiroticus* and *P. ridibundus/P. kurtmuelleri*, we did not detect clear species-specific trophic separation. Moreover, partitioning of beta diversity indicated that most dietary dissimilarity among individuals was driven by prey turnover rather than nestedness, suggesting that frogs consumed largely distinct prey sets rather than subsets of a shared pool.

Previous studies on *Pelophylax* frogs consistently report broad and opportunistic feeding strategies, with diets dominated by terrestrial and aquatic native or invasive invertebrates (Karaica et al., 2016; Plitsi et al., 2016; Pesarakloo et al., 2017; Breka et al., 2024) or even vertebrates (Országhová et al., 2003; Nicolaou et al., 2014; Katsiyiannis and Tzoras, 2020; Khashab and Jablonski, 2025). Our results are in line with this general pattern, confirming that both *P. epeiroticus* and *P. ridibundus/P. kurtmuelleri* exploit a wide spectrum

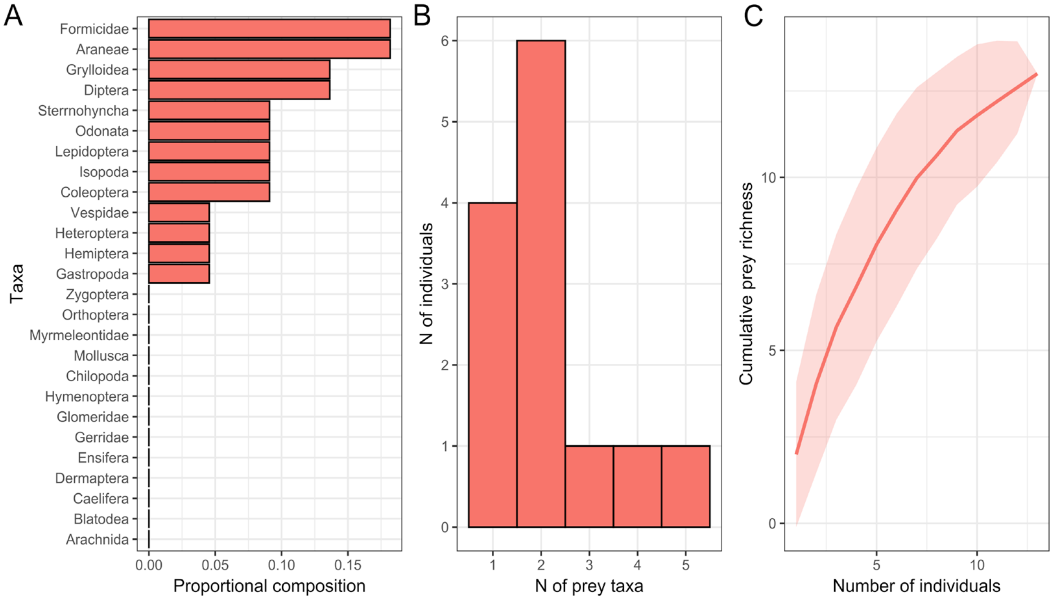

Figure 3. Summary of prey diversity detected in the stomach contents of *Pelophylax epeiroticus* (*n* = 13). (A) Proportional composition of prey taxa across all individuals. (B) Distribution of individual prey richness, expressed as the number of distinct prey taxa per individual. (C) Species accumulation curve showing cumulative prey richness as a function of the number of sampled individuals. The shaded area represents the 95% confidence interval.

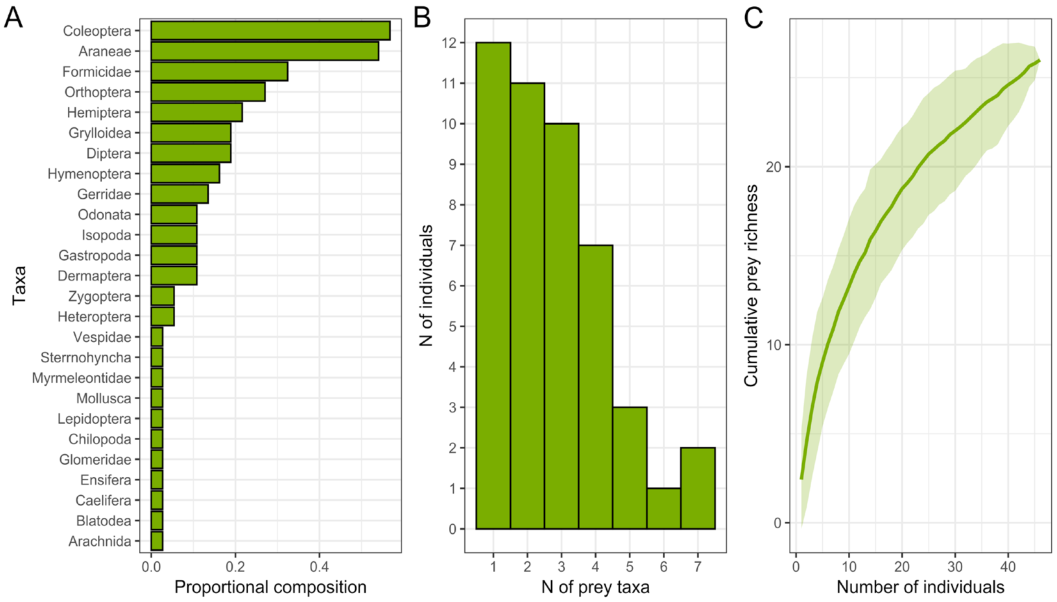

Figure 4. Summary of prey diversity detected in the stomach contents of *Pelophylax ridibundus/P. kurtmuelleri* (*n* = 46). (A) Proportional composition of prey taxa across all individuals. (B) Distribution of individual prey richness, expressed as the number of distinct prey taxa per individual. (C) Species accumulation curve showing cumulative prey richness as a function of the number of sampled individuals. The shaded area represents the 95% confidence interval.

of arthropod prey without clear interspecific separation. Similar to findings in other regions and taxa, the frogs included in this study exhibited a high degree of dietary flexibility, reflecting their role as generalist predators in freshwater and riparian ecosystems (Pille et al., 2022). In comparison with other studies, our samples revealed a significantly lower average number of prey items per individual (overall = 2.62; *P. epeiroticus* = 2.15; *P.*

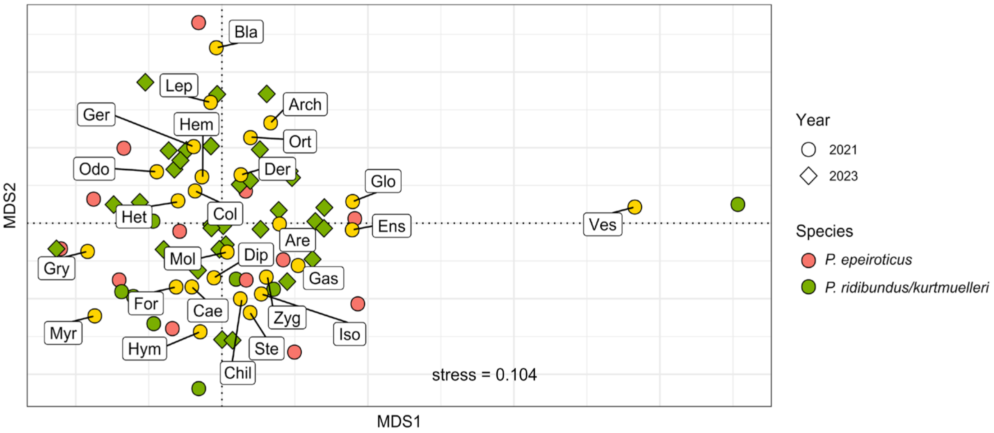

Figure 5. NMDS ordination of stomach content data based on Jaccard dissimilarity. Each point represents an individual frog, colour-coded by species (*Pelophylax epeiroticus* in red, *P. ridibundus/P. kurtmuelleri* in green) and shaped according to the year of sampling (2021 = circles, 2023 = diamonds). Prey taxa are plotted as weighted centroids (yellow) and labelled with taxon abbreviations (see Fig. 2A for full names).

ridibundus/P. kurtmuelleri = 2.76), whereas values of 5.86 and 9.87 were reported by Pesarakloo et al. (2017) and Balint et al. (2010), respectively, both of which identified prey items to the lowest possible taxonomic level. Importantly, this study provides the first detailed dietary data for the endemic Epirus Waterfrog *P. epeiroticus*, thereby filling a critical gap in knowledge for one of the least studied European anurans. Similar to other congeners, *P. epeiroticus* displayed a generalist trophic profile.

A striking pattern emerging from our dataset is the high level of dietary turnover among individuals, with β_{JTU} values indicating that dissimilarities were almost exclusively driven by prey replacement rather than by nested subsets of a shared prey pool. In practical terms, most frogs consumed distinct prey combinations, even when sampled from the same locality. Such individuality in foraging behaviour has been documented in several anuran taxa (Araújo et al., 2011) and is increasingly recognised as an important component of trophic ecology. The strong individual-level variation observed here is consistent with opportunistic predation, where prey choice is largely determined by immediate availability rather than by fixed preferences.

Several methodological constraints of our study should be acknowledged. First, the use of presence/absence data reduces the resolution of dietary analysis, as quantitative information on prey abundance and biomass was not available. Second, soft-bodied prey items are likely underrepresented due to rapid digestion, a common issue in stomach content studies (Hyslop, 1980). Third, although sampling was carried out in the same season, the surveys were conducted in different years, which may have introduced unaccounted inter-annual variation in prey availability. Finally, the number of *P. epeiroticus* examined was relatively small, limiting detailed comparisons. Moreover, the accumulation curves indicate that additional sampling could yield a more comprehensive list of prey taxa. Future research should therefore aim to increase sample sizes, incorporate quantitative dietary data, or apply DNA metabarcoding approaches, which would provide a more comprehensive view of trophic diversity and allow testing of seasonal and inter-annual effects.

In conclusion, our results highlight the opportunistic and flexible trophic ecology of *Pelophylax* frogs in Greece, characterised by broad prey spectra and strong individual-level variation. By documenting the first dietary records for the endemic *P. epeiroticus*, this study contributes valuable baseline knowledge for a species of conservation concern. The generalist feeding strategy observed suggests that *P. epeiroticus* is capable of exploiting diverse prey resources, which may enhance its ecological resilience. At the same time, reliance on invertebrate prey communities links its persistence to environmental conditions that influence insect diversity and abundance. Understanding such trophic interactions is essential not only for elucidating the ecological role of waterfrogs in freshwater ecosystems but also for assessing their potential vulnerability to anthropogenic habitat changes and broader shifts in prey availability.

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