Piquet *et al. Ecological Processes* (2025) 14:62
https://doi.org/10.1186/s13717-025-00630-z

Ecological Processes

RESEARCH **Open Access**

The cascading impact of an invasive snake on arthropod communities

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Abstract

Background The depletion of birds and mammals by invasive snakes is known to trigger top-down trophic cascades in recipient ecosystems. However, the indirect effects of island reptile depletion by invasive snakes remain largely unexplored, despite reptiles being an integral component of island food webs and serving as important prey for snakes. We assessed the impacts of the invasive species *Lampropeltis californiae* on arthropod communities on the island of Gran Canaria, mediated through the depletion of the three endemic reptile species of the island.

Methods First, we analysed the dietary components of endemic reptiles using metabarcoding techniques to identify the most and least consumed arthropod orders. Next, we estimated ground-dwelling arthropod abundances in invaded and uninvaded sites via pitfall sampling to assess the effects of ground-dwelling endemic reptile depletion on arthropod fauna. Then, we conducted plant beating and sweeping samplings to assess the potential effects of this depletion on vegetation-dwelling arthropods. Finally, we compared the abundances of the most and least consumed arthropod orders in invaded and uninvaded sites.

Results Our results confirmed the existence of a trophic cascade. Invaded sites exhibited higher abundances of arthropod orders that were predominantly consumed by the endemic reptiles. As expected, the abundances of arthropods weakly associated to the endemic reptiles—*i.e.*, least consumed orders and vegetation-dwelling arthropods—were predominantly influenced by seasonal changes and did not show a significant response to the invasive snake presence.

Conclusions Our findings highlight the significant ecological consequences of *L. californiae* at the ecosystem level on Gran Canaria, revealing impacts that extend beyond direct predation on the endemic reptiles and induce a trophic cascade. More broadly, our results demonstrate the capacity of invasive snakes to disrupt native ecosystems by depleting native reptiles.

Keywords Canary Islands, Endemic reptile, Invasive predator, *Lampropeltis californiae*, Metabarcoding diet index, Trophic cascade

Introduction

Native communities and ecosystems worldwide are being drastically altered by the accelerating introduction of invasive species (IPBES 2019, 2023). Invasive predators are of great concern as they decimate resident species (Bellard et al. 2016; Doherty et al. 2016), often triggering trophic cascades that cause major shifts in ecosystem dynamics and configuration (Schoener et al. 2002; White et al. 2006; David et al. 2017). Trophic cascade strength usually depends on species diversity at each trophic level, with stronger cascades often observed in ecosystems that have lower species diversity (Schoener and Spiller 2010). On islands, where ecological redundancy is low (Whittaker and Fernández-Palacios 2007) and the biota is extremely susceptible to invasive predators (Bellard et al. 2017;

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Russell et al. 2017), trophic cascades could be particularly severe and aggravated when reptiles are involved, as they are a crucial element of island food webs (Schoener et al. 2002; Beard et al. 2021). Despite the importance of understanding the indirect effects of invasive predators in an insular context, trophic cascades are generally understudied (White et al. 2006; David et al. 2017), especially when invasive snakes are involved.

The rate of snake introductions has exponentially risen since the beginning of the twentieth century (Kraus 2009), with 48% of the 129 established populations worldwide occurring on islands (Capinha et al. 2017). The few cases studied have shown that they are causing dramatic effects on island vertebrates, which can deregulate native communities and trigger cascading indirect effects (Rogers et al. 2012; Freedman et al. 2018). For instance, bird predation by the invasive brown treesnake (*Boiga irregularis*) on Guam led to the massive loss of insectivorous species (Wiles et al. 2003), which produced a concomitant increase in spider and ant abundance (four times higher than in uninvaded neighbouring islands) (Rogers et al. 2012; Freedman et al. 2018). Direct impacts also extend to native and endemic herpetofauna (amphibians and reptiles). For instance, *B. irregularis* led to the demise of native geckos and skinks on Guam (Rodda and Fritts 1992), the horseshoe whip snake (*Hemorrhois hippocrepis*) caused the decline or local extinction of the endemic Ibiza wall lizard (*Podarcis pityuensis*) (Montes et al. 2022), and the common wolf snake (*Lycodon capucinus*) is most likely linked to the extinction of 80% of the endemic herpetofauna on Christmas Island (Emery et al. 2021). In spite of that, the indirect effects of island herpetofauna depletion by invasive snakes have been overlooked thus far.

Island reptiles are generalist predators that opportunistically feed on a broad range of resources, including numerous plants and invertebrates, vertebrate carrion, and marine-derived subsidies (*e.g.*, Kartzinel et al. 2015; Alemany et al. 2023; Pinho et al. 2025). Arthropods often play a major role in island reptile diets, although their importance varies seasonally with fluctuations in their abundance and the availability of alternative food sources (Rodríguez et al. 2008; Gil et al. 2020; Alemany et al. 2023). Manipulative experiments in neotropical island ecosystems have shown that the removal of reptiles leads to population outbreaks of their most-consumed prey, including arthropods from the orders Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera and Blattodea (Pacala and Roughgarden 1984; Dial and Roughgarden 1995; Beard et al. 2021). However, the specific context of these experiments limits our ability to infer the broader ecological consequences of reptile removal across diverse island systems.

On Gran Canaria, the invasive *Lampropeltis californiae* primarily preys on the three endemic reptiles (Monzón-Argüello et al. 2015) that constitute the entire island herpetofauna (some introduced species have been recorded but without naturalized populations; Gobierno de Canarias 2025). Snake predation pressure reduced the number of individuals of the Gran Canaria giant lizard (*Gallotia stehlini*) by 93.5%, the Gran Canaria skink (*Chalcides sexlineatus*) by 82.8%, and Boettger's wall gecko (*Tarentola boettgeri*) by 52.1% (Piquet and López-Darias 2021). Considering that these three species play a critical role in the island food webs by consuming a broad range of ground-dwelling arthropods (Mateo et al. 2022), their depletion could lead to an increase in arthropod abundance and the subsequent alteration of invertebrate communities. In this context, the main aim of our research was to determine the existence of a potential trophic cascade initiated by *L. californiae* on Gran Canaria. To do so, we used a set of invaded sites where endemic reptiles had been significantly depleted, and a group of environmentally equivalent and uninvaded sites with abundant reptile populations. We applied DNA metabarcoding to first identify the arthropod orders most consumed by the endemic reptiles in uninvaded sites. We then quantified and compared the abundance of ground-dwelling orders between invaded and uninvaded sites to determine the existence of a trophic cascade affecting endemic reptile main prey. We also surveyed vegetation-dwelling arthropod orders and compared their abundance to assess whether the cascade extended to these taxa less directly associated with the endemic reptiles. We finally cross-checked the dietary components of the three endemic reptiles with data on arthropod abundance to determine if snake presence affected only the groups most consumed by the endemic reptiles, thereby confirming the existence of a trophic cascade. Under this scenario, our hypothesis is that the depletion of endemic reptiles by *L. californiae* produces a trophic cascade leading to their most consumed prey (expectably the same as for other island reptiles) to attain higher abundances in invaded sites, whereas seldom consumed arthropods would remain unaffected.

Materials and methods

Sampling sites

We evaluated trophic cascades in five invaded and five uninvaded sites on Gran Canaria (Fig. 1). We located invaded sites in areas holding depleted or no endemic reptile populations, as reported by Piquet and López-Darias (2021), and abundant *L. californiae* captures and sightings recorded for at least five years (Fig. 1; GESPLAN 2024). We conversely placed uninvaded sites in areas known to hold abundant populations of endemic

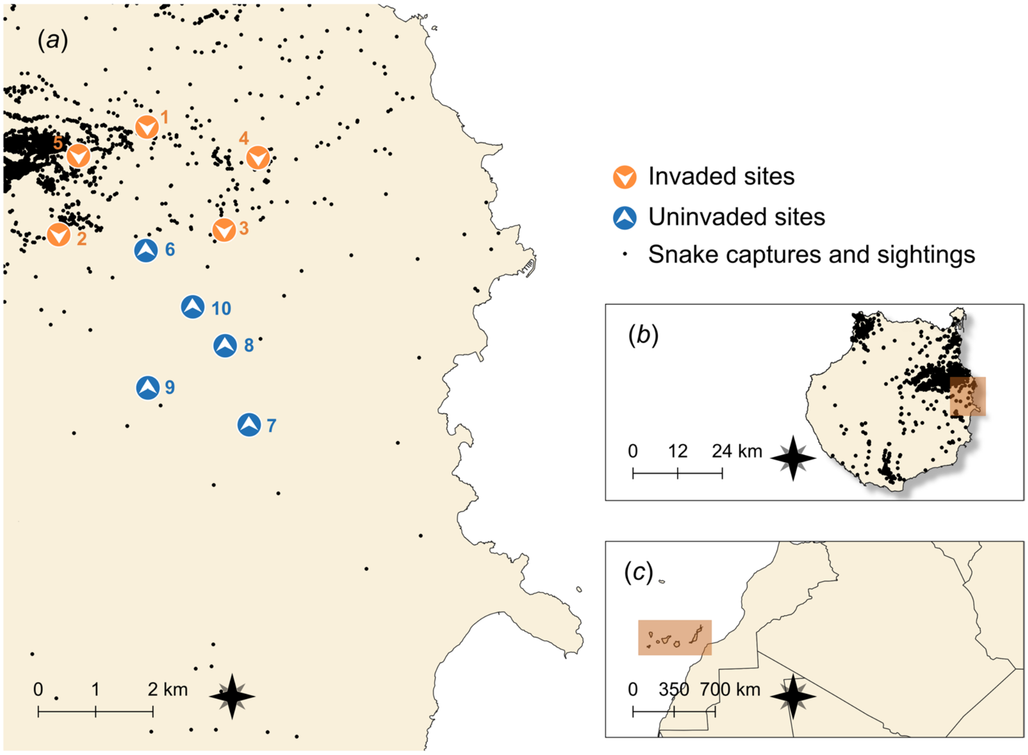

Fig. 1 Invaded (orange; 1–5) and uninvaded (blue; 6–10) study sites on Gran Canaria (**a**), with insets showing the location of the study area on the island (**b**) and the location of the Canary Islands (**c**). Black dots represent *Lampropeltis californiae* records from 2009 to 2019, according to GESPLAN (2024)

reptiles and at a distance of 643 ± 344 m (mean ± SD; ranging from 307 to 1173 m) from any snake record (Fig. 1; GESPLAN 2024)—*i.e.*, exceeding the distances covered by the daily movements and average home range of *L. californiae* in the island (Maestresalas et al. 2023). We located all sites within an area of less than 13 km^2 on the eastern slope of Gran Canaria, sharing altitudinal range, climatic conditions, and vegetation (see Supporting Information 1), so that main differences between sites were related to the presence of *L. californiae* rather than to other environmental factors.

Identifying consumed arthropod orders

No information was available on the diet of *G. stehlini*, *C. sexlineatus*, and *T. boettgeri* in our study sites, which were previously studied only in other ecosystems or islands (Brown 1990; López-Jurado 1998; Roca 1999; Carretero et al. 2006; Gil et al. 2020). Thus, to analyse the diet of these species in the ecosystem where the study sites were located and account for seasonal trophic variation, we captured each reptile species in uninvaded sites—following common procedures (Piquet et al. 2022)—in May, August, and November 2019 (*i.e.*, at the beginning and the end of the dry season, and during the humid season, respectively). We relegated diet analysis to uninvaded sites to prevent any effect of *L. californiae* on the endemic reptile diet. In each capture session, we collected faeces from 4–12 individuals of each species by gently pressing their abdomens and dropping samples directly into individually identified 1.5 ml tubes with 99% dehydrated ethanol—thus minimizing contamination and maximizing DNA detection (Ando et al. 2020). As diet analysis at the individual reptile level was not the focus of this study, we combined faeces of an equivalent number of adult males and females of each species in a *c.* 200 mg single sample for each species, site, and season—15 samples per species (1 per site, 5 per season) (see Supporting Information 2: Table S2.1 for the number of individuals per sample). We stored the sample tubes at − 20 °C until we conducted DNA extraction using the E.Z.N.A. extraction kit (Omega Bio-Tek, Inc. Norcross, GA, U.S.A.). We sent the extracted samples to AllGenetics & Biology SL (www.allgenetics.eu) for subsequent genetic analyses and bioinformatic processing. Libraries were prepared by amplifying a *c.* 100 bp fragment of the 16S rRNA region using the primers IN16STK-1F-mod (3′ TRA ACT CAG ATC ATG TAA 5′) and IN16STK-1R-mod (3′ TTA GGG ATA ACA GCG TWA 5′) (Kartzinel and Pringle 2015;

Gil et al. 2020). Libraries were then purified, equimolarly pooled, and sequenced in a fraction of a NovaSeq PE250 lane (Illumina) (see Supporting Information 3 for detailed genetic procedures). Raw reads were quality-checked, trimmed, and filtered before being used for taxonomic assignment via BLASTN 2.8.1+and for the creation of the Operational Taxonomic Unit (OTU) table (see Supporting Information 3 for a complete description of bioinformatic processing). Because reference sequences are lacking for a considerable number of arthropod families and most species from the Canary Islands, we used order as the taxonomic level to classify reptiles' diet, thus avoiding the occurrence of questionable assignments at lower levels.

To describe the importance of the different arthropod orders in reptiles' diet, we used the final OTU table to calculate three complementary indices for all the species pooled together, following Deagle et al. (2019) and Xiong et al. (2017): (1) relative read abundance data for each order (RRA; *i.e.*, the quotient between the number of reads per order and the total number of reads per sample), (2) percentage frequency of occurrence of each order (%FOO; the number of samples from the total that contained the order), and (3) percentage of occurrence (POO; the number of samples that contained the order divided by the sum of orders' occurrences). We calculated all parameters for each season and for all seasons pooled together. These indices are the most frequently used metrics to analyse animal diets in metabarcoding studies (Deagle et al. 2019; Ando et a. 2020), yet they suffer from specific biases and a lack of integration of available information that has led to a substantial divide in the scientific community (reviewed in Ando et a. 2020). Traditional diet studies use the index of relative importance (IRI) to integrate the number of preyed items and their frequency of occurrence (Pinkas et al. 1970), but no equivalent exists for genetic data. Thus, with the purpose of integrating both approaches and counterbalancing their deficiencies, we additionally designed a modified index of relative importance (hereafter, mIRI) to be applied to metabarcoding data (Eq. 1).

$$\mathrm{mIRI} = \frac{RRA_i \times POO_i}{\sum_{i=l}^{T} RRA_i \times POO_i} \times 100, \tag{1}$$

where i is any given food item and T is the total number of food items detected (orders in this case). Finally, to quantitatively define the most and the least consumed arthropod orders, we performed a k-means cluster analysis with total mIRI values for the whole year using the 'kmeans' function, including 100 random configurations to obtain the best output.

Detecting the trophic cascade

We surveyed ground-dwelling arthropods by placing 20 pitfall traps for seven days at each site (Emerson et al. 2017; Montgomery et al. 2021). As arthropod abundance also varies seasonally (Montgomery et al. 2021), we repeated this sampling in May–June, August, and November 2020 to account for the influence of season in our sampling (see Supporting Information 4 for further sampling details). We retrieved pitfall contents into individually labelled tulle bags, and examined them under a stereomicroscope at least twice to morphologically sort all arthropods and quantify their number at the level of order, using taxonomic keys or with the assistance of entomological experts from IPNA-CSIC. We did not use higher taxonomic resolution due to the significant taxonomic knowledge gaps for the Canary Islands arthropofauna—particularly relevant for groups such as the hyper-diverse Hymenoptera and Diptera (Lobo and Borges 2010)—thus avoiding unreliable classifications (Derraik et al. 2002; Krell 2004).

Since any alteration in food webs can cascade across trophic levels (Mooney et al. 2010; Schoener and Spiller 2010), we complementarily sampled vegetation-dwelling arthropods using foliage-beating and plant-sweeping samplings (Emerson et al. 2017; Montgomery et al. 2021). We conducted one beating and sweeping sampling at each site during both daytime and night-time—respectively defined as the period after sunrise and before twilight, and from 30 min after sunset to 1 a.m.—with at least 24 h between each sampling event. These samplings either coincided with pitfall sampling periods or occurred less than a week after trap retrieval. To avoid interferences, we performed all beating and sweeping samplings away from active pitfall traps. We retrieved beating and sweeping samples into separate tubes with 99% dehydrated ethanol with the help of an entomological aspirator. For beating samplings, we additionally noted down the plant species on which we sampled arthropods. We later examined beating and sweeping samples following the same procedure as for pitfalls (see Supporting Information 4 for further sampling details).

To detect the effect of *L. californiae* on arthropod abundance and link it to the clustering output of consumed orders, we ran generalized linear mixed models using the package *glmmTMB* (Brooks et al. 2017). We ran a model for each order and method using snake presence (invaded *vs.* uninvaded), season, and their interaction as fixed factors, and sampling site as a random factor. We also included trap ID as a random factor for pitfall data models, nested within sampling site, as trap location did not vary between seasons. We included all fixed factors in the dispersion model (*dispformula* argument) to account for variation in the dispersion parameter and significant heterogeneity of the variance of the dependent variable (Brooks et al. 2017). To account for data overdispersion (Lindén and Mäntyniemi 2011), we specified a negative binomial distribution with a quadratic parametrization term for all models. To prevent model convergence issues, we excluded all orders occurring in less than 3% of the samples per sampling method and those with an average abundance below 0.05 individuals per sample in invaded or uninvaded sites. We also discarded the use of plant species as a model predictor for the same reason, after confirming that the proportion of samples from each species was comparable across invaded and uninvaded sites (see Supporting Information 5: Table S5.1). After checking model residuals using the *DHARMa* package (Hartig 2022), we obtained model main effects by using type-II Wald Chi-square tests via 'Anova' function (Langsrud 2003), and performed post hoc pairwise comparisons using the *emmeans* package (multivariate *t* adjustment used as *P* value correction for multiple comparisons) (Lenth 2023).

We carried out all analyses in R 4.4.1 (R Core Team 2025). We show all results as mean ± SD.

Results

Consumed arthropod orders

Metabarcoding analyses revealed that the endemic reptiles preyed upon 24 arthropod orders across all seasons, with Diptera, Coleoptera, Hymenoptera and Hemiptera ranking higher in all diet indices (Table 1), but showing high seasonal variation (see Supporting Information 6: Table S6.1 and Fig. S6.1). The cluster analysis resulted in two groups, the four most-consumed orders constituting the first group, with the 20 remaining orders clustered in a second group (the least consumed orders) (Table 1).

Overall abundance of arthropod orders

Arthropod surveys and subsequent morphological identification allowed detecting the presence of 34 orders in all study sites, which included 87.5% of the orders consumed by the endemic reptiles (Opiliones, Polydesmida, and Strepsiptera were not detected). When pooling samples from all sites, Hymenoptera was the most abundant order, followed by Araneae, Hemiptera, Entomobryomorpha, Coleoptera, and Diptera, although abundance varied seasonally (Supporting Information 7: Table S7.1 and Fig. S7.1).

Table 1 Relative read abundance (RRA), percentage frequency of occurrence (%FOO), percentage of occurrence (POO), and modified index of relative importance (mIRI) (see main text for further details on index calculations) per order of Arthropoda detected in the diet of the endemic reptiles—*Gallotia stehlini*, *Chalcides sexlineatus* and *Tarentola boettgeri*—pooled together. All indices were calculated using data from all seasons pooled together (see Supporting Information S6 for seasonal calculations). Arthropods are ordered in highly or less consumed orders (see cluster analysis in Supporting Information S3)—*i.e.*, high and low total mIRI, respectively—and coloured accordingly in dark or light blue, respectively

Order	RRA	%FOO	POO	mIRI
Diptera	24.74	88.89	10.70	26.35
Coleoptera	17.57	93.33	11.23	19.64
Hymenoptera	16.49	97.78	11.76	19.32
Hemiptera	14.34	88.89	10.70	15.27
Lepidoptera	9.21	84.44	10.16	9.32
Araneae	4.06	77.78	9.36	3.78
Zygentoma	4.42	53.33	6.42	2.82
Psocoptera	1.80	37.78	4.55	0.81
Orthoptera	1.51	22.22	2.67	0.40
Embioptera	0.76	13.33	1.60	0.12
Ixodida	0.31	8.89	1.07	0.03
Neuroptera	0.34	6.67	0.80	0.03
Strepsiptera	1.00	2.22	0.27	0.03
Mesostigmata	0.10	15.56	1.87	0.02
Opiliones	0.08	15.56	1.87	0.02
Isopoda	0.04	15.56	1.87	0.01
Blattodea	0.04	8.89	1.07	0.00
Mantodea	0.03	11.11	1.34	0.00
Sarcoptiformes	0.03	8.89	1.07	0.00
Thysanoptera	0.04	4.44	0.53	0.00
Entomobryomorpha	0.01	11.11	1.34	0.00
Polydesmida	0.02	4.44	0.53	0.00
Siphonaptera	0.01	2.22	0.27	0.00
Lithobiomorpha	0.00	2.22	0.27	0.00
Other	3.04	55.56	6.68	2.03

Arthropod abundance in invaded and uninvaded sites

Arthropod order abundances differed between invaded and uninvaded sites for three out of the four most consumed orders (Diptera, Hymenoptera and Hemiptera), while the abundances of Coleoptera and all the least consumed orders remained similar between sites (although differed mostly depending on the season; Fig. 2, Table 2). The year-round abundance of Diptera was 26.73% higher in invaded than in uninvaded sites, a difference that rose up to 84.12% during November (Fig. 2a; see Supporting Information 8 for site-level differences). Hemiptera and Hymenoptera were more abundant in invaded sites in November, with an increase of 319.45% and 106.08% of the abundance, respectively, in invaded sites in comparison with uninvaded sites (Fig. 2b and c; see Supporting Information 8 for site-level differences). Invaded and uninvaded sites also differed in the pattern of seasonal abundance of certain orders, *i.e.*, invaded sites exhibiting either stable abundances or seasonal abundance

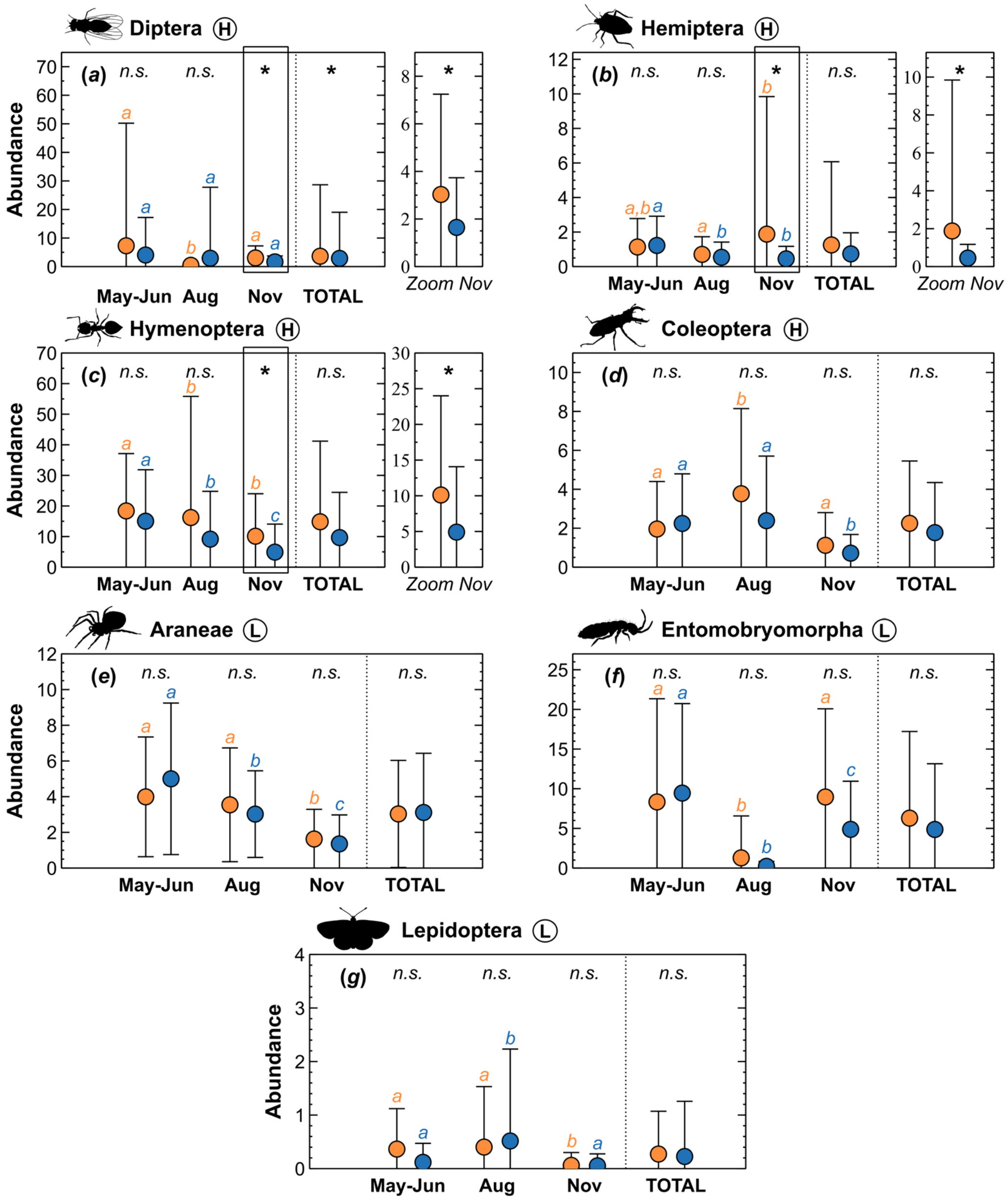

Fig. 2 Abundance (average number of indivuduals per sample; mean ± SD) of Diptera (**a**), Hemiptera (**b**), Hymenoptera (**c**), Coleoptera (**d**), Araneae (**e**), Entomobryomorpha (**f**), and Lepidoptera (**g**) captured for each season (May–Jun, Aug, Nov) and all seasons pooled together (TOTAL) using pitfall traps in sites invaded (orange) and uninvaded (blue) by *Lampropeltis californiae*. Abundance was quantified through morphological identification under a stereomicroscope. High-consumption and low-consumption orders are identified with H and L next to the panel title, respectively. Differences between invaded and uninvaded sites in each season or throughout the year are signalled with an asterisk in the upper part of each panel (*n.s.* indicates no significant differences). Seasonal pairwise differences for invaded and uninvaded sites are separately indicated in each case with different letters above each mean and error plot. All silhouettes were obtained from www.phylopic.org

peaks, absent from uninvaded sites where most groups' abundance decreased over the seasons (Fig. 2; see Supporting Information 8 for site-level differences). This shift occurred in all of the most consumed orders and the least consumed Araneae, Lepidoptera, and Entomobryomorpha (Fig. 2; see Supporting Information 8 for site-level differences).

Invaded and uninvaded sites showed differences in the vegetation-dwelling arthropod orders, although these were limited to three orders (Table 2). Diptera

Table 2 Results of the Generalized Linear Mixed Models carried out to detect differences in the abundance of arthropod orders for each sampling method, *i.e.,* pitfall, beating and sweeping. Wald χ^2 and *P* values are shown for main effect factors from GLMMs—snake presence (snakes), season and their interaction (snake × season). Arthropod orders are presented grouped in the most (high) and the least (low) consumed groups (see Supporting Information 7: Table S7.1 and Fig. S7.1). Bold numbers represent significant results

Sampling	Group	Order	Snakes		Season		Snakes × season	
			χ^2	*P*	χ^2	*P*	χ^2	*P*
Pitfall	High	Coleoptera	1.22	0.270	**87.59**	**0.000**	**9.94**	**0.007**
		Diptera	**3.97**	**0.046**	**57.76**	**0.000**	**7.89**	**0.019**
		Hemiptera	1.48	0.223	**22.75**	**0.000**	**18.62**	**0.000**
		Hymenoptera	1.90	0.168	**68.63**	**0.000**	**9.78**	**0.008**
	Low	Araneae	0.00	0.975	**132.65**	**0.000**	**7.73**	**0.021**
		Embioptera	1.14	0.285	**10.35**	**0.006**	2.38	0.304
		Entomobryomorpha	0.09	0.770	**169.63**	**0.000**	**25.72**	**0.000**
		Isopoda	3.25	0.071	**35.99**	**0.000**	1.12	0.571
		Lepidoptera	0.73	0.394	**30.51**	**0.000**	**6.27**	**0.043**
		Mesostigmata	0.76	0.384	**39.18**	**0.000**	1.65	0.438
		Psocoptera	1.81	0.179	**29.48**	**0.000**	0.20	0.905
		Sarcoptiformes	1.00	0.317	**86.90**	**0.000**	0.45	0.800
		Thysanoptera	0.41	0.523	**48.65**	**0.000**	0.66	0.721
		Zygentoma	1.44	0.231	**111.16**	**0.000**	0.09	0.954
Beating	High	Coleoptera	0.04	0.834	**79.14**	**0.000**	2.37	0.306
		Diptera	3.69	0.055	**29.58**	**0.000**	4.86	0.088
		Hemiptera	0.54	0.462	0.03	0.985	0.92	0.631
		Hymenoptera	0.62	0.431	**17.29**	**0.000**	3.31	0.191
	Low	Araneae	1.25	0.264	**14.15**	**0.001**	0.54	0.762
		Lepidoptera	0.02	0.896	**5.73**	**0.057**	0.51	0.776
		Psocoptera	0.02	0.877	**11.01**	**0.004**	1.70	0.428
		Sarcoptiformes	0.04	0.839	5.23	0.073	0.88	0.643
Sweeping	High	Coleoptera	0.46	0.496	**24.01**	**0.000**	2.30	0.317
		Diptera	**5.40**	**0.020**	**60.39**	**0.000**	1.03	0.596
		Hemiptera	0.28	0.599	**17.08**	**0.000**	**8.14**	**0.017**
		Hymenoptera	0.84	0.359	**33.29**	**0.000**	0.50	0.778
	Low	Araneae	2.29	0.130	**27.21**	**0.000**	0.46	0.793
		Lepidoptera	0.70	0.402	**18.43**	**0.000**	5.87	0.053
		Mantodea	1.63	0.202	**20.91**	**0.000**	2.26	0.323
		Psocoptera	0.24	0.626	**33.89**	**0.000**	2.48	0.289
		Sarcoptiformes	0.50	0.482	**15.77**	**0.000**	0.00	1.000
		Thysanoptera	0.29	0.591	3.38	0.185	**11.48**	**0.003**

was 46.80% less abundant in sweeping samples from invaded sites (Fig. 3; see Supporting Information 8 for site-level differences), whereas the direction of the differences in Hemiptera abundance between sites shifted across months (Table 2, Fig. 3a and b; see Supporting Information 8 for site-level differences). Additionally, the abundance of Thysanoptera, a low-consumption order, was seasonally affected by the presence of *L. californiae* (Table 2), although no differences were found when comparing sites in each season, nor sites separately across the year (Fig. 3c; see Supporting Information 8 for site-level differences).

Discussion

Detection of a trophic cascade on Gran Canaria

Our results indicate that *L. californiae* causes a trophic cascade affecting ground-dwelling arthropods through the depletion or extirpation of their predators, the native reptile community. Nearly all the most consumed arthropod orders were more abundant in invaded than

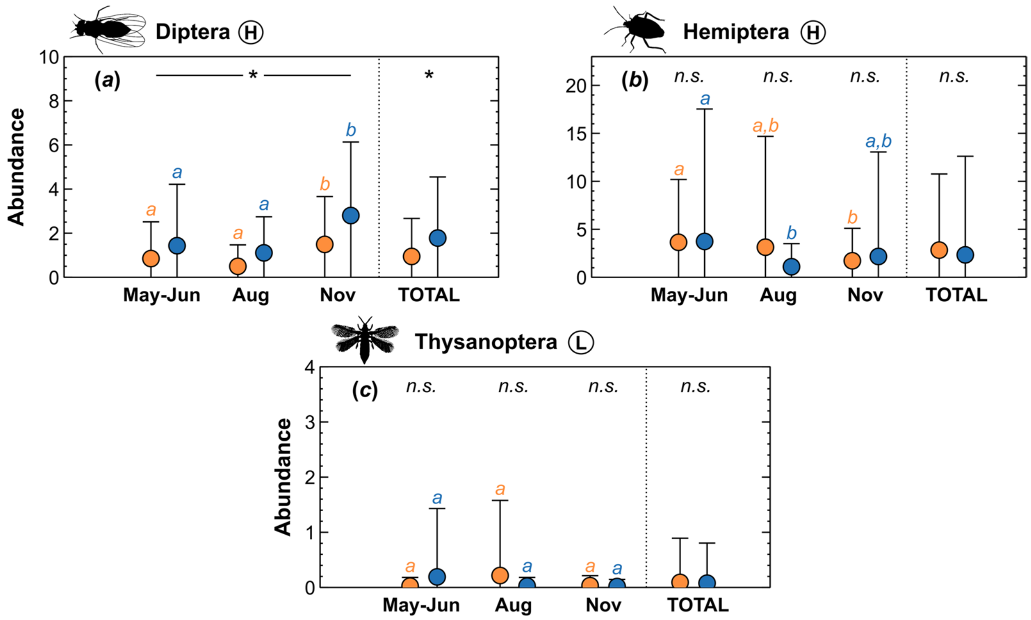

Fig. 3 Abundance (average number of individuals per sample; mean ± SD) of Diptera (**a**), Hemiptera (**b**) and Thysanoptera (**c**) captured for each season (May–Jun, Aug, Nov) and all seasons pooled together (TOTAL) using sweeping samplings in sites invaded (orange) and uninvaded (blue) by *Lampropeltis californiae*. Abundance was quantified through morphological identification under a stereomicroscope. High-consumption and low-consumption orders are identified with H and L next to the panel title, respectively. Differences between invaded and uninvaded sites in each season or throughout the year are signalled with an asterisk in the upper part of each panel (*n.s.* indicates no significant differences). Intra-seasonal differences are not shown in panel (**a**) due to the absence of significant interaction between snake presence and season in Diptera. Differences among seasons for invaded and uninvaded sites are separately indicated in each case with different letters above each mean and error plot. All silhouettes were obtained from www.phylopic.org

in uninvaded sites in November, while all the least consumed ground-dwelling orders and most vegetation-dwelling arthropods were unaffected by the presence of the invasive snake. This is consistent with previous research on trophic cascades, whose effects often show strong seasonality due to numerous abiotic and biotic factors involved (*e.g.*, Schoener and Spiller 2010; Piovia-Scott et al. 2017), while being dampened for those trophic levels less directly related to the missing predators (Dial and Roughgarden 1995; Schoener et al. 2002; Beard et al. 2021).

Seasonal differences between invaded and uninvaded sites may relate to temporal shifts in reptiles' diet due to food source availability and abundance (Gil et al. 2020; Alemany et al. 2023). For instance, reptiles on Gran Canaria may have consumed arthropods more intensely during autumn and winter months, when fleshy fruits become less abundant, as detected for other endemic lizards in the archipelago (Rodríguez et al. 2008). Seasonal variation in reptiles' diet would have led to a pronounced reduction on prey abundance in uninvaded sites with abundant reptile populations, whereas this effect would have been milder or absent in areas lacking these endemic predators. Alternatively, considering the observed seasonal differences matched the onset of the wet season in the region (Luque Söllheim et al. 2024), ground-dwelling Diptera, Hemiptera and Hymenoptera may have also started to experience small population bursts related to seasonal rains, as observed in other semi-arid ecosystems (*e.g.*, Fischer et al. 2022). The increase in the abundance of the most consumed orders would have been naturally dampened or delayed by the endemic reptiles in uninvaded sites, while being unchecked in those sites where these natural predators are absent. Lastly, these differences may also result from seasonal rainfall altering food webs, as rainfall in semi-arid environments can modulate the direction and strength of trophic interactions within native communities by influencing the abundance of their components (Deguines et al. 2017).

Since the endemic reptiles of Gran Canaria are ground-dwelling species (Mateo et al 2022) with generalist feeding habits comparable to that of other insular lizards (*e.g.*, Alemany et al. 2023; Pinho et al. 2025), these endemic predators would also exhibit an opportunistic feeding strategy, primarily feeding on the most abundant and accessible taxa (*i.e.,* arthropods showing similar ecological habits). In contrast, less abundant orders (*e.g.*, Blattodea) and those with ecological habits that differ from those of the reptiles—such as fossorial or plant-associated taxa like Entomobryomorpha or Thysanoptera

(Potapov et al. 2022)—played a less significant role in their diets. This would explain the lack of differences between invaded and uninvaded sites for these taxa, for which the depletion of endemic reptile population would have had a limited impact. However, trophic cascades are complex processes, particularly hard to define in arthropod communities as they can simultaneously act as both predators and prey (Mooney et al. 2010). Therefore, less consumed arthropod orders may have experienced indirect effects from the alteration of intermediary taxa, leading to complex responses across the food webs. Although precisely tracking these effects would require a deeper knowledge of ecological networks within arthropod communities in the Canary Islands, these likely explain the phenological shifts observed in certain ground- and vegetation-dwelling orders. Regardless of the mechanisms behind these phenological shifts, our results match similar findings from other snake-invaded systems as Guam, where the depletion of insectivorous birds by *B. irregularis* allows web spiders to remain abundant all year long, whereas neighbouring snake-free islands show seasonal reductions of spider abundance (Rogers et al. 2012), highlighting the role of island reptiles in shaping food webs. In fact, the similarity between the arthropod taxa affected by trophic cascades on Gran Canaria and those identified in manipulative experiments on Caribbean islands (Dial and Roughgarden 1995; Beard et al. 2021) suggests the existence of a general pattern that could extend to other snake invasions.

The utility of the modified index of relative importance (mIRI)

Massive sequencing techniques are remarkably useful non-invasive tools to study animal diet (Ando et al. 2020), yet the transformation of sequencing data into quantitative data on biomass or relative importance remains unresolved (Deagle et al. 2019). RRA, %FOO or POO are commonly used indices (Xiong et al. 2017; Ando et al. 2020), although their appropriateness is still under debate (Deagle et al. 2019). Occurrence-based indices (%FOO and POO) are less sensitive to biological and technical factors affecting DNA amplification, effectively incorporate rare food items, and facilitate comparisons across diet studies (Ando et al. 2020). These indices, however, lack of quantitative information, are unrelated to prey biomass, and tend to inflate the relevance of rare prey items, all of which is effectively addressed by RRA (Deagle et al. 2019; Ando et al. 2020).

Herein, we propose the use of mIRI as a potential solution to this controversy, as it adequately incorporates POO (or %FOO, as they produce the same result) and RRA into a single index. Building upon traditional diet index calculations (Pinkas et al. 1970), mIRI expands conservative occurrence-based indices with semi-quantitative information, providing data at finer resolution, dampening biases related to DNA amplification, and incorporating rare prey without overestimation. Additionally, mIRI would allow studies performed at a higher taxonomic resolution to incorporate biomass data as in the original IRI used in traditional diet studies (Pinkas et al. 1970). Furthermore, by integrating both types of indices, mIRI would help to bridge current scientific division regarding the quantification of animal diet from genetic data (Ando et al. 2020). Considering the potential benefits delivered by this index, we encourage the scientific community to consider this new metric and quantitatively evaluate its performance compared to other indices.

Analytical challenges in the study

Trophic cascades are complex processes whose interpretations present significant challenges. Those involving arthropods are especially difficult to interpret, as their communities and associated bottom-up and top-down effects can be affected by numerous factors such as climate-related seasonality (Rogers et al. 2012; Deguines et al. 2017) and plant assemblages (Minor et al. 2021). Moreover, sampling methods and taxonomic resolution can substantially shape the observed community composition and abundance (Montgomery et al. 2021), further complicating the characterization of trophic cascades. In our study, the small geographical scale minimized climate and vegetation variability, while we comprehensively sampled ground- and vegetation-dwelling orders with complementary methods appropriately designed to characterize these communities (Montgomery et al. 2021).

However, three limitations can be extracted from our study. First, complementary sampling methods would have been needed to detect certain orders of arthropods and obtain representative estimates of their actual abundances (Montgomery et al. 2021). Second and more important, large taxonomic knowledge gaps on arthropod communities (Lobo and Borges 2010; Stork 2018) prevented us from describing trophic cascades at higher resolution. The complementary use of metabarcoding techniques for arthropod surveys could have helped in dealing with this issue, as observed in previous research on reptile diet (Gil et al. 2020). However, the implementation of such techniques was obstructed by the current paucity of reference sequences at lower taxonomic level and the difficulty in translating read counts into accurate abundance estimates (Ando et al. 2020), which was of particular relevance to characterize the trophic cascade. Similarly, incorporating morphological identification into the analysis of reptile diet would have allowed complementing our data with information on prey abundance. Yet, previous research illustrates that these are time-consuming techniques that allow the detection of only a portion of the consumed prey and have lower taxonomic resolution than metabarcoding analyses (Gil et al. 2020). Third, despite our precautions in selecting uninvaded sites, the cryptic behaviour of *L. californiae* (Maestresalas et al. 2023) prevents us from definitively excluding its presence in all selected sites. However, considering the magnitude of snake impacts on the endemic reptiles (Piquet and López-Darias 2021), their high abundance in uninvaded sites strongly suggests that *L. californiae* was either absent or present at low abundances, having limited influence on food webs. Notwithstanding potential methodological limitations, our study demonstrates that *L. californiae* exerts significant impacts on native arthropod communities, underscoring the ecological consequences of the depletion of endemic reptiles.

Potential ecological and socioeconomic repercussions

Considering that *L. californiae* rapidly expands across Gran Canaria (GESPLAN 2024) and trophic cascades can reverberate across ecological and spatial barriers (Knight et al. 2005; García-Callejas et al. 2019), our results underline the pernicious effects that *L. californiae* imposes on native ecosystems, which are expected to extend throughout the island as the invasion progresses. Arthropods support crucial functions in terrestrial ecosystems (Yang and Gratton 2014), thus the trophic cascade identified here could result in deeper impacts on native ecosystems and their dynamics. For instance, the alteration of arthropod communities could affect native vegetation by disturbing plant mutualistic services, plant reproductive success (Knight et al. 2006), or herbivory dynamics (Mooney et al. 2010), as phytophagous Hemiptera have significantly increased their abundances as an indirect result of this invasion (Potapov et al. 2022). Furthermore, *L. californiae* top-down effect may also cause socioeconomic problems on the island, as some of the orders whose abundances have increased are amongst the most important agricultural pests (*e.g.*, Hemiptera; Culliney 2014) or are vectors affecting human health (*e.g.*, Diptera; Tolle 2009). Although peaks in abundance mostly occurred in a single season, this might translate in seasonal outbreaks of arthropod-borne diseases and agricultural pests comparable to those observed elsewhere (*e.g.*, Kirchner et al. 2013; Stratton et al. 2017). Given the relevance of these impacts, further studies exploring this trophic cascade would allow to delve deeper into its ecological and social consequences. We anticipate that additional studies will likely reveal even more extensive consequences.

Conclusions

Our study demonstrates that the depletion of the endemic reptiles by *L. californiae* on Gran Canaria results in increased arthropod abundance through a trophic cascade, potentially leading to significant ecological and socioeconomic consequences for the island. Globally, this study extends existing evidence on the capacity of invasive snakes to trigger cascading ecological effects, which have predominantly involved native birds and mammals (Rogers et al. 2012, 2017; Hoyer et al. 2017; Willson 2017; Freedman et al. 2018). Furthermore, our findings highlight the substantial impacts of ectothermic predators on native communities, an influence that has traditionally been underestimated compared to endothermic organisms (Borer et al. 2005). Despite the increasingly evident impacts of invasive snakes, including trophic cascades, these organisms have been largely overlooked in the field of biological invasions. This oversight is particularly concerning given the widespread establishment of invasive snakes in numerous regions, including many islands (Kraus 2009; Capinha et al. 2017), where similar ecological disruptions could occur. Therefore, we advocate for greater attention to the global impacts of invasive snakes.

Abbreviations

%FOO	Frequency of occurrence
mIRI	Modified index of relative importance
OTU	Operational taxonomic unit
POO	Percentage of occurrence
RRA	Relative read abundance

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-025-00630-z.

Supplementary Material 1.

Acknowledgements

We are deeply thankful to all the people that helped us during invertebrate sorting, particularly the identification made by entomological experts at IPNA-CSIC (Heriberto López, Daniel Suárez, and Antonio J. Pérez). We also thank Mercedes López for her help in DNA extractions for reptile diet analysis. We address our sincerest gratitude to the Gobierno de Canarias, Cabildo de Gran Canaria, and GESPLAN S.A., which provided us with relevant information, logistic support, and lodging. A special mention to thank Fred Kraus, Shane R. Siers, Anthony Herrel, Robert N. Reed for their extensive comments on the PhD from which this manuscript derives.

Author contributions

Conceptualization: JCP, MLD; Funding acquisition: JCP, MLD; Project administration: MLD; Methodology: JCP, BM, MLD; Investigation: JCP, BM, MLD; Formal analysis: JCP, MLD, Supervision: MLD; Visualization: JCP, MLD; Writing—original draft: JCP, MLD; Writing—review & editing: JCP, BM, MLD.

Funding

This research was supported by Fundacion BBVA, within the 2018 call of "Ayudas a Equipos de Investigación Científica en Ecología y Biología de la Conservación", as well as by the Gobierno de Canarias within the Lamproimpact agreement. At the time of this study, JCP was funded by a doctoral fellowship supported by the Agencia Canaria de la Investigación, Innovación y Sociedad de la Información and the European Social Fund (Operational Programme of the Canary Islands 2014–2020—Priority Axis 3: Priority Theme 74, 85%) and MLD was funded by a research contract from the Transference Plan of the Cabildo de Tenerife, under the registration mark "Tenerife 2030" (P. INNOVA 2016-2021). This research had all necessary authorizations provided by Cabildo de Gran Canaria (555/2019), and Gobierno de Canarias (No. 2020/12858), as well as ethical clearance provided by Gobierno de Canarias (CEIBA2020-0423).

Availability of data and materials

The dataset and code supporting the conclusions of this article are available in the Figshare repository, https://doi.org/10.6084/m9.figshare.18209756.v2.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

Authors have no competing interest to disclose.

Received: 22 January 2025 Accepted: 14 July 2025

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