IN THE BELLY OF THE BEAST: HOW DIETARY CHANGES MAY HAVE ENHANCED THE ABILITY OF EASTERN RED-BACK SALAMANDERS (*PLETHODON CINEREUS*) TO INVADE NEWFOUNDLAND, CANADA

BY

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Abstract

The island of Newfoundland, Canada, has no native amphibians or reptiles. Since colonization, however, six species have been introduced. The Eastern Red-backed Salamander (*Plethodon cinereus*) is the most recently described of these non-native herptiles with a self-sustaining population occurring in Conception Bay South. Little is known about their origins, invasion history, or invasive ecology. The introduction of species outside of their native range can lead to detrimental environmental changes, particularly for species that reach high biomass and drive energy flow within ecosystems - like the Eastern Red-backed Salamander. I posit that this salamander's successful establishment and proliferation may have been mediated by pre-existing invasive prey communities creating open niches (i.e., the Invasional Meltdown hypothesis), as well as by dietary shifts which may have allowed these salamanders to capitalize on a wider variety of local prey (i.e., Niche Breadth Invasion Success hypothesis). To test these hypotheses, I examined the stomach contents of 133 Eastern Red-backed Salamanders from Newfoundland and identified their prey. Stomach contents were obtained through dissection, with prey items identified to the lowest possible taxonomic level, using dichotomous keys, field guides, and crowd-sourced iNaturalist consultation. In total, I assessed 1073 individual prey items. I then compared the composition of the invasive diet to the native range, using data I generated from a systematic literature review. As expected, the invasive population's diet became more generalised (i.e., broadening their niche breadth) and pre-established invasive prey comprised a substantial proportion of what was eaten (i.e., ~67% of the volume of prey items consumed, accounting for ~36% of the total individual prey items). My research provides foundational knowledge on what native prey are being consumed by this introduced predator, as well as some of the pre-existing conditions (e.g., prior invertebrate invasions) that may have allowed the salamanders to colonise a previously salamander-free Newfoundland.

Introduction

Invasive species are a globally pervasive threat, due to their negative impacts on native populations, biological communities and the economic strain they cause, related to productivity loss, human health effects, and the high cost of preventing, managing, and/or eradicating invasive populations (Simberloff & Holle, 1999; Gurevitch & Padilla, 2004; Bacher et al., 2018). Invasive species can cause ecological damage by disrupting trophic relationships, nutrient cycling, and resource availability for native species (David et al., 2017). For example, Cane Toads, *Rhinella marina*, native to South America, have been introduced across the globe and are a known to be a highly destructive, successful invader (Lowe et al., 2000). In Australia alone, Cane Toads have expanded their range to approximately 1.2 million km^2 of the northeastern Australian coast line since 1935. This invasion not only impacts lower trophic levels, competing with the ever-growing toad population (Shine, 2014), but the potent toxic secretion of cane toads severely affected apex predators (e.g., monitor lizards; *Vanarus* spp.) leading to widespread trophic cascades and potentially irreversible ecological damage (Doody et al., 2017). Similarly, Brown Tree Snakes, *Boiga irregularis*, were introduced to Guam in the 1940s, which led to a significant loss in the island's avifauna including the extirpation of 12 bird species and declines of 90% for another eight species (Rodda et al., 1992; Wiles et al., 2003). These examples point to the clear ecological threat invasive populations can pose, and they can also come at significant socio-economic cost as well (Bacher et al., 2018). For example, Giant Hogweed, *Heracleum mantegazzianum*, is an invasive plant that has had accidental introductions throughout Europe and North America, where its thick canopy cover outcompetes native plants for light as it forms dense monotypic stands (Page et al., 2006). This shift in the vegetative community, results in high density stands of Giant Hogweed destabilising riverbanks and damaging the spawning habitats of economically-important salmonid fish in Great Britain (Caffrey, 1999). Furthermore, Giant Hogweed secretions cause a phototoxic reaction resulting in burns, blistering, and hyperpigmentation of exposed skin (Knudsen, 1983), leading to inflated health care costs (Cuddington et al., 2022). This is not to assert that all invasive populations innately cause negative ecological or economic impacts (i.e., some can be viewed as neutral or potentially beneficial within certain contexts; Boltovskoy et al., 2018), but the potential for negative impacts to arise does exist and the uncertainty around this is greater for novel taxa establishing an invasive population for the first time. Unfortunately, within the modern era, and despite increasing efforts to curtail their spread, the introduction and establishment of new invasive populations across the globe continues to increase each year due to expanding human activity, ever-growing transportation networks, and anthropogenic habitat change (Seebens et al., 2017). As such, it has become increasingly clear that understanding the factors that contribute to the proliferation of biological invasions, as well as the mechanisms that increase a species invasion success, is of the utmost importance (Kowarik, 1995).

Although the rates of new biological invasions continue to steadily increase (Seebens et al., 2017), the outcome for most invasions is failure - owing to the many abiotic and biotic barriers encountered during the process (Blackburn et al. 2011). Invasive populations form after non-native individuals progress through a series of 'invasion stages', whereby they must be able to survive transport to a new location, survive within the new habitat, reproduce and maintain a self-sustaining population, and expand their range beyond the site of initial establishment (Richardson et al., 2000; Blackburn et al., 2011). Between each of these invasion stages are ecological barriers (e.g., an inability to survive transport or successfully breed within the habitat), that can lead to invasion failure (Blackburn et al., 2011). In fact, it is expected that owing to these barriers most potential biological invasions fail, especially after accidental introductions, however the specific factors leading to these invasion failures are understudied (Zenni & Nuñez, 2013). For example, although the Cane Toad is one of the most significant vertebrate invaders of the last century (Shine, 2014; Doody et al., 2017), even they have suffered failed introductions in both Mauritius and Tanzania (Greathead, 1971) - albeit little is known as to why. In addressing which specific factors allow for invasion failures or successes, we can hone our abilities to predict where biological invasions may occur or better manage them as they form. For example, the small littoral snail, *Littorina saxatilis*, has highly successful invasive populations within North American intertidal zones, yet introductions into the Mediterranean basin failed due to areas of increased salinity (Bosso et al., 2022). Bosso et al. (2022) findings providing valuable insight into the factors limiting an otherwise highly invasive species from increasing their range. Through understanding the drivers that lead to either invasion failure or success, we can increase our understanding of the mechanics of biological invasions; this has led to an entire network of hypotheses centred on how non-native populations can overcome the barriers between invasion stages (see Enders et al., 2020). These invasion hypotheses encompass various factors that are associated with enhancing invasive potential, spanning biological, ecological, and evolutionary influences (Enders et al., 2020). For example, some invasions are thought to have been successful because the species had a high degree of phenotypic plasticity (e.g., Plasticity hypothesis; Richards et al., 2006), or are no longer suppressed by their evolved predators which are absent in the invaded ecosystem (e.g., Enemy Release hypothesis; Keane & Crawley, 2002), or the species possess certain traits, like defences, that provide them a survival over native taxa (e.g., Novel Weapons hypothesis; Callaway & Ridenour, 2004). Another branch of these invasion hypotheses, however, pertains to the fundamentals of whether or not a non-native population is capable of integrating into a new ecosystem, relating to questions surrounding how they may be able to fit into a new niche space.

One of the leading means by which invasive animal populations can become established and spread outward from their introduction site is related to their ability to capitalise on novel resources or leverage a generalist diet (Marvier et al., 2004; Peterson & Vieglais, 2001; David et al., 2017). A broad ecological niche, including flexible diet and habitat use, are assets that can support a species invasion (Marvier et al., 2004). Dietary studies offer the possibility to examine an invasive species' dietary niche and its position in a food web. Invasive species damage food webs by creating new trophic links; they disrupt top-down and bottom-up effects, and increase lateral competition (David et al., 2017; White et al., 2006). If a potential invasive population is capable of modifying their diet to more efficiently integrate into a novel food web (e.g., increasing their dietary niche breadth), they can increase their invasive potential (i.e., Niche Breadth Invasion Success hypothesis; Vazquez, 2006). For example, African Clawed Frog (*Xenopus laevis*) is a globally invasive amphibian with a generalist diet (Measey et al. 2012); however, during its invasion into France it was seen to expand its dietary niche breadth compared to populations in its native Southern African range, which was theorized to have increased its successful spread (Courant et al., 2017). Similarly, when the dietary niche breadths of invasive populations of the Round Goby, *Neogobius melanostomus*, and Tubenose Goby, *Proterorhinus semilunaris*, were compared, the more successful invader within the Laurentian Great Lakes (i.e., *N. melanostomus*) was seen to have a broader and more plastic diet (Pettitt-Wade et al., 2015). Although expanding a species' dietary options or proclivities may enhance some populations' abilities to invade, this trend is not seen across all invasions (Pettitt-Wade et al., 2018) and can even be antithetical (i.e., dietary niche constriction; see Jackson et al., 2016). Regardless, dietary plasticity may not be sufficient to allow establishment of potential invasive population if much of the evolved niches are filled and high functioning (MacArthur, 1970). To overcome this challenge, invading populations may require some form of disturbance that disrupts a niche's *status quo* to create resource opportunities (MacArthur, 1970; Hobbs & Huenneke, 1992; Jeschke & Strayer, 2006), or for novel opportunities to be created by the presence of additional invasive taxa (Simberloff and Holle 1999).

The Invasional Meltdown Hypothesis posits that the success of one invasive species can facilitate the establishment and proliferation of other introduced organisms within a given ecosystem (Simberloff and Holle 1999). This suggests a relationship between different invasive species occupying the same novel habitat, wherein the presence of pre-existing invaders can create favorable conditions for the success of the establishing species (Simberloff & Holle, 1999; Green et al., 2011). The invasive species interactions can increase pollination and dispersal of invasive plants (Mandon-Dalger et al., 2004) or physically modify ecosystems in a way that is favorable for an invasive population (e.g., creating open or under-used niches or resources), providing the opportunity for the recently arrived population to overcome fundamental barriers to establishment (Gurevitch & Padilla, 2004; Marvier et al., 2004; Blackburn et al., 2011). For example, a global review on invasive American Bullfrog, *Lithobates catesbeianus*, populations found that invasive crayfish are a common and dominant prey group in their diet, and 76% (n = 169/222) of the examined established bullfrog populations co-occur with invasive crayfish (Liu et al., 2018). Invasive predator-invasive prey relations can also result in mutual benefits. Red-whiskered Bulbul, *Pycnonotus jocosus*, were introduced to the Mascarene Islands in the late 1800s (Cheke, 1987), whereupon invasive flora (e.g., Soapbush, *Miconia crenata*) comprised much of the birds' diet (Linnebjerg et al., 2009). The existence of invasive fruit-bearing plants allowed the avian invaders to flourish, but it also further expanded the range and density of the invasive plants as the growing invasive bird population acted as seed dispersers (Cheke, 1987; Linnebjerg et al., 2009). Similarly, the invasion of Crazy Yellow Ants, *Anoplolepis gracilipes*, to Christmas Island caused the decline of multiple species of native land crabs through predation, which opened niche space for a secondary invasion by the Giant African Land Snail, *Lissachatina fulica* (O'Dowd et al., 2003; Green et al., 2011), while fowling mussels, *Dreissena spp*., in the Laurentian Great Lakes hardened the soft-sediment habitat thereby promoting the invasion of Ponto–Caspian Amphipod, *Echinogammarus ischnus*, into areas that were previously unsuitable (Bially & Macisaac, 2001; Ricciardi, 2001). As such, the positive feedback loop that an Invasional Meltdown hypothesis (Simberloff and Holle 1999) scenario can create, provides a strong line of evidence for why rates of non-native species introductions continue to increase annually (Seebens et al. 2017). It also provides evidence for the value of managing, and potentially limiting invasion populations of seemingly benign or neutrally impactful invasive species – as they may promote the invasion of more threatened taxa in the future.

As countries endeavour to better understand their growing invasive species communities, particular attention should be paid to regions that represent invasive hotspots (O'Neill et al., 2021; Schneider et al., 2021). For example, the island of Newfoundland hosts one of the densest assemblages of domestic invasive species (i.e., taxa that is native to areas elsewhere in a country, but not to the region of interest; Kamada et al., 2013) in Canada. This may be best underscored by the island herpetofauna community. Newfoundland has no native amphibians or reptiles, however since colonization, six species have been introduced. The most recent addition to this invasive herpetofauna community came from recent descriptions of the Eastern Red-backed Salamander, *Plethodon cinereus*, which was found to be maintaining a self-sustaining population near Conception Bay South (Baxter-Gilbert et al., 2022). Given that many of the invasive amphibians and reptiles of

Newfoundland are considered dietary generalists, like American Toad, *Anaxyrus americanus*, (Cloyed & Eason, 2017), Eastern Garter Snake, *Thamnophis sirtalis*, (Arnold, 1978), and Eastern Red-backed Salamander (Bondi et al., 2019), these invasions offer an important opportunity for the study of how changes in dietary niche breadth and the composition of invasive/non-native prey relate to these successful invasions. This may be particularly pertinent for the most recently described invasive amphibian to Newfoundland, Eastern Red-backed Salamander, as it has the potential to represent a significant threat to ecosystem function through disrupting energy flow and increasing intraguild competition (see Baxter-Gilbert et al., 2022). However, we currently lack information on this invasive population's diet - a primary driver of negative ecological impacts - or how they successfully colonised this novel landscape.

Here, my study will examine how the diet of the Eastern Red-backed Salamander may have changed during their invasion of Newfoundland and whether their successful establishment may also relate to the use of invasive prey items. I hypothesize that their diet within the invasive range will have a significantly wider niche breadth than within their native range (i.e., testing the Niche Breadth Invasion Success hypothesis; Vázquez, 2006) and that a high proportion of their diet will consist of prey from pre-existing invasive/non-native invertebrate communities (i.e., testing the Invasional Meltdown hypothesis; Simberloff and Holle, 1999), which may have both contributed to their invasion success. To test these hypotheses, I will test a set of predictions related to: (1) a dietary comparison between invasive and native populations and (2) the dietary composition of the invasive population. To do this, I will first analyze the stomach contents of salamanders collected from Newfoundland and contrast it to a robust dataset from across the species known distribution. I predict that the invasive, Newfoundland population will have a significantly wider dietary niche breadth compared to populations across their native range, by expanding the taxonomic richness and diversity of their prey. This dietary expansion is expected to have occurred to allow them to better capitalize on novel food sources, and is akin to what has been seen in other invasive amphibian populations (e.g., African Clawed Frogs invading France; Courant et al., 2017). Finally, I predict that the invasive salamander population's diet will consists of a high proportion of invasive/non-native invertebrates in abundance (> 15% by count, akin to what was seen in invasive bullfrog; Liu et al., 2018), but also in biomass (> 30% by volume).

Methods

Study system

Study species

Eastern Red-backed Salamander is a medium length (total length adult 5-12 cm) terrestrial Plethodontid salamander, native to northeastern North America (Conant & Collins, 1998). They are commonly found in and around wooded areas, often associated with damp habitats and cover objects, such as leaf litter, logs, sections of bark, rocks, and an array of anthropogenic debris (Heatwole, 1962; Conant & Collins, 1998). These salamanders play a vital role in maintaining the ecological balance of forested habitats, as they can achieve high biomass, drive energy flow within ecosystems through nutrient cycling, and exert strong intraguild competition (McKenny et al., 2006; Hickerson et al., 2012, 2017). In forests, they can reach exceptionally high biomass, representing a dominant taxa (McKenny et al., 2006). They can also act as a top-down regulator for the detritivore communities (Hickerson et al., 2017), while simultaneously influencing bottom-up effects within food webs as they are prey for numerous secondary consumers (Brodie et al., 1979). Given this species' ecology, they are often considered quite common across their range. Despite their broad eastern distribution in Canada, they were absent from the island of Newfoundland; however climatic niche modelling of the species' distribution noted that although the species was presumed to be not present on Newfoundland (i.e., as they were not native to the region) the current available climate was suitable enough to sustain populations (Moore et al., 2018). As such, the recent description of a self-sustaining population in Newfoundland was, in-part not wholly surprising – given the habitat suitability (Moore et al. 2018) and the region's density of other invasive amphibians (Baxter-Gilbert et al., 2022) – yet, nothing is currently known about the invasion history of this population, nor their impact on native species.

Study Site and Field Collections

The forest ecosystem around Conception Bay South, Newfoundland, Canada (centred 47.5073° N, 52.9965° W), is found within the Maritime Barrens Forest ecoregion, which is dominated by Balsam Fir forests, contains thick mossy forest floors, has interspersed open heathland, and is characterised by cooler, foggy summers and relatively mild winters (DFFA, 2021). Such habitats as similar, but not identical, to the habitats within Nova Scotia, the closest native population, which are described as deciduous, coniferous, and mixed forests (Gilhen, 1984).

From May 18th to June 13th 2022, researchers from Mount Allison University (J. Baxter-Gilbert and J. Riley) collected 133 Eastern Red-back Salamanders from Conception Bay South. Collections involved haphazard surveys that were conducted in both anthropogenically modified habitats (e.g., backyards, gardens, lawns, and rubbish piles) and natural areas (e.g., upland forests, stream, and treed edges around wetlands). Surveys consisted of flipping cover objects (e.g. debris, logs, rocks, sections of bark, and refuse) and visually inspecting to determine if a salamander was present underneath. When a salamander was found, it was captured by hand, sexed (male, female, juvenile), measured (i.e., snout-vent-length (SVL) in mm), and humanely euthanized in a MS-222 (tricaine mesylate) bath, containing 500 mg/L of MS-222 and buffered with sodium bicarbonate to a pH ~7. Once the salamander was determined to be deceased, it was immediately preserved in 95% ethanol, then transferred to a -20°C freezer, and sent to Mount Allison University for frozen storage until dissection.

During these surveys it was found that each individual salamander observed associated with anthropogenically disturbed habitats, such as backyards and gardens, while none were found in more natural/wild habitats in this area (i.e., mossy forest floors containing abundant natural cover, like logs and rocks) (J. Baxter-Gilbert *pers. comm*). Furthermore, the samples collected included neonates, juveniles, and adults, which suggests a sustained breeding population and supports the assertions made by Baxter-Gilbert et al. (2022).

All specimens were handled and collected under the permission of the Wildlife Division of Newfoundland and Labrador (Scientific Research Permit # WLR2022-35). Ethics approval through the Mount Allison University Animal Care Committee (Animal Ethics Protocol # 103181).

Data Collection

Gut Content Removal and Processing

An incision was made along the salamander's ventral surface with small scissors. Connective tissue was pulled apart so the stomach could be exposed, and it was removed intact by cutting the distal end of the esophagus and proximal end of the small intestine. Once the stomach was removed it was cut open and flushed with 95% ethanol under a dissecting microscope. Prey items were sorted and identified to the lowest possible taxonomic level using keys, field guides, and crowd-sourced consultation on the web-based data repository iNaturalist (www.inaturalist.ca). Each prey item was identified and categorized as either native or invasive using publicly available reference material (e.g., CESCC, 2020). The length (L) and width (W) of every prey item was measured using a caliper nearest 0.01 mm. Volume (V) of each prey item was calculated as an ellipsoid using the formula:

$$V = \frac{4}{3} * \pi * L * W^2$$

Prey items within one sample that were slightly digested, broken down, or otherwise separated were collated together to count as single prey item, for more conservative estimates. For example, if three separate legs were recovered from the same type of prey item, and no missing legs were seen on more intact members of that taxa, then the unaccounted-for legs were clustered and counted as a single individual. If length and width measurements were unable to be taken due to a more progressed digestive state, then data was taken from the average of that prey type from measured individuals across their level of taxonomic identification. This was done to ensure consistency and comparability across my dataset. After all identifications, counts, and prey measurements were complete from a given stomach's content, salamanders and the prey items recovered from their stomachs were returned to vials of 95% ethanol and stored in a -80°C freezer (each salamander and their stomach content were now stored separately).

Literature Review

Search Strategy and Selection Criteria

To locate publications involving Eastern Red-backed Salamanders and their diet within their native range, I undertook a systematic literature review using the Systematic Reviews and Meta-Analysis (PRISMA) approach as described in Page et al., (2021). I searched two research repositories, ISI Web of Science Core Collection and Scopus, on Oct 11, 2023, using a string search with key words related to species name and dietary analysis, these search terms included:

Web of Science: (TS=("eastern red-backed salamander" OR "redback salamander" OR "Plethodon cinereus") AND TS=("diet*" OR "gut?content" OR "stomach?content"))

Scopus: TITLE-ABS-KEY (("eastern red-backed salamander" OR "redback salamander" OR "Plethodon cinereus") AND ("diet*" OR "gut?content" OR "stomach?content"))

I also searched Herpetological Review manually using the *find* function (i.e., Ctrl + F) within a collation of all the available issues published between 1967-2023, searching with the term "*Plethodon cinereus"*. I then reviewed each article and extractedextracted dietary studies to add to the previously compiled list. The addition of the Herpetological Review, which is not indexed on Web of Science, was done because it often is a source of dietary reporting on the natural history of herpetofauna.

The results of both searches were imported into Covidence systemic review software which removed duplicates (Covidence Systemic Review Software, 2024). Two reviewers independently screened titles and abstracts (J. Riley and myself). Conflicts were resolved by consensus through discussion with a third reviewer (J. Baxter-Gilbert). I reviewed 126 articles and retained studies that contained data on Eastern Red-backed Salamander relating to: (1) general diet, (2) diet composition, (3) studies conducted on wild individuals (i.e., not in laboratory conditions), and (4) those not from a duplicate article. Using these four criteria 111 articles were excluded, the 14 remaining articles continued through to data extraction.

Data Extraction

For the retained articles, I extracted data on the count, types, and composition of salamander prey per location. If required dietary data was unavailable from within the main article or supplementary materials, I contacted the authors to request missing data. In one paper, only graphical representations of the diet were available, so I used package *metaDigitize* (Pick et al., 2019) in RStudio version 2023.6.2.561 (R Core Team, 2023) to extract average prey per individual and then converted to number of prey items per site. Also, if only average prey per individual was available, I converted the value by multiplying by the number of individuals at a site to generate more comparable data.

Across the retained articles, different studies used different taxonomic levels for prey identification. During my collation of this data I standardized the taxonomic levels to allow for comparisons, however this standardization led to a loss of specifics about the prey as increasing taxonomic levels were unable to be inferred. For example, where some studies included identification specificity down to the species-level or genus-level (such as my own, presented here), many others only identified prey down to the order-level. For this reason, comparison between the Newfoundland salamander population and those from across the native range are conducted primarily at the order-level; with some exceptions made for specific taxa well known in dietary studies (e.g., separating Hymenoptera into Hymenoptera and Hymenoptera: Formicidae, to account for bees/wasp and ants separately).

In addition to diet, I also extracted location data. Latitude and longitude for each study site was extracted directly from the methods section of each article or from the original datasets supplied by the articles' authors. If the locations were unavailable, they were estimated using site descriptions and approximated using Google Maps to determine an estimate of the studies' location. The purpose of the geographic data was to ensure that if the prey diversity did vary between the invasive and native population, it was not a product of a previously established cline in the invertebrate diversity of the diet (e.g., if prey diversity in the native range increases with latitude (Hillebrand, 2004), then I would naturally expect the Newfoundland population to increase regardless of native/invasive status of the salamander population).

Data Analysis

All analysis was conducted in RStudio version 2023.6.2.561 (R Core Team, 2023).

Dietary Comparison Between Invasive and Native Populations

To test whether the diet differs between the invasive population of Eastern Red-backed Salamander to conspecific across their native range, I analysed the proportions of each prey item recovered from invasive and native salamanders. I combined all the native range data to represent an average diet of the species within its native range. I compared the original proportions in two ways, using (1) a Kolmogorov-Smirnov goodness of fit test and (2) a Chi-square test within package *ggstatsplot* (Patil, 2021). To compare differences in proportion of the diet represented by each prey type, the counts between the native range dataset and the invasive population data were standardized by finding the proportion within the separate ranges and then multiplying by 100,000. This allowed for prey counts with small proportions to be preserved. Differences for each prey type were compared through Chi-Square tests using package *ggstatsplot* (Patil, 2021). I calculated the Shannon-Weiner diversity index for each sample location using the package *vegan* (Oksanen et al., 2022).

Dietary Composition of the Invasive Population

I examined the proportion of invasive and native prey within the diet of the invasive salamander population using two metrics: abundance (representing count data of individuals) and biomass (repressing the volume of the prey consumed). I compared the abundance (i.e., percentage of invasive prey item count relative to total number of prey items recovered) and tested for a significant difference from 50% using a Chi-Square test. To determine if the invasive population is consuming a statistically higher volume of native or invasive prey, I ran a Wilcoxon Ranked Sum test and compared the volume of invasive prey within the diet of each salamander to the volume of native prey within each salamander. Additionally a Vacuity Index (i.e., percentage of empty stomachs relative to the total number of stomachs examined; Hyslop, 1980) was calculated for the invasive population.

Results

Literary Analysis

Data was collected from 14 studies and 20 unique locations in the native range and (Figure 1). All studies sampled the diets of Eastern Red-back Salamanders, 5 studies used dissection and 9 used gastric lavage for diet retrieval. In total data from the diets of 1318 salamanders was accumulated from the literature.

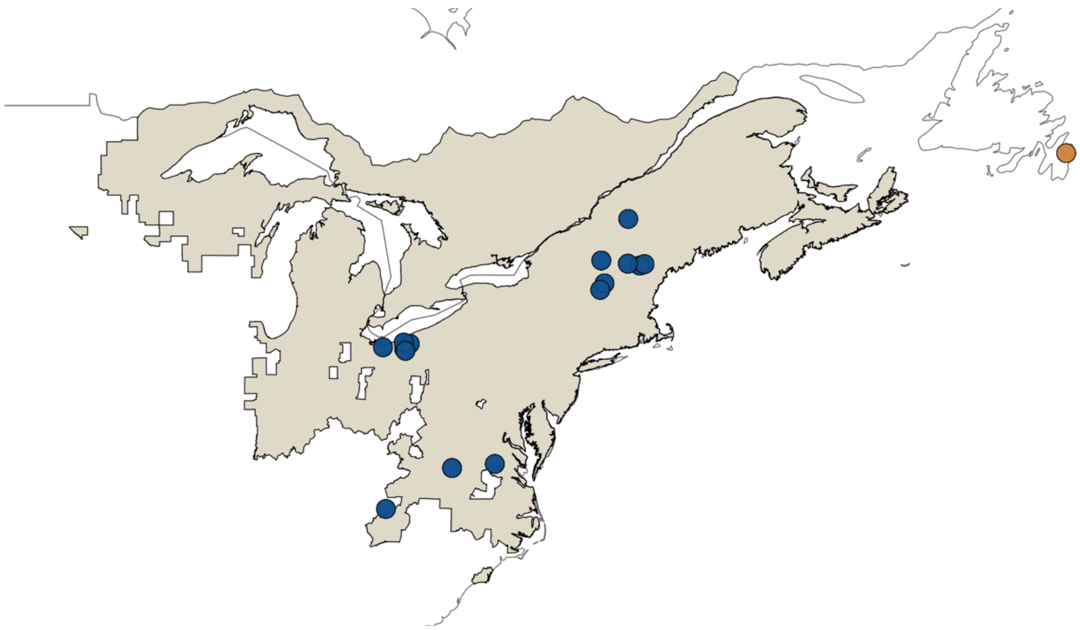

Figure 1. Locations of studies used in data analysis. Native range of Eastern Red-backed Salamanders, *Plethodon cinereus*, in grey, study sites used in data collection in blue within native range (n = 20), location of Newfoundland population in yellow (n = 1).

Dietary Comparison Between Invasive and Native Populations

In the comparison of the diet make-up between the native and invasive range I found a statistically significant difference between the populations when using a Kolmogorov-Smirnov goodness of fit test ($p < 0.001$) and when using a Chi-squared test (x^2_{34} = 1748.56, $p < 0.001$). There was a statistically significant difference in the proportions of every prey item between the diets of the invasive and native populations (Table 1; Figure 2). The invasive site in Newfoundland had the highest Shannon-Weiner Diversity index of 2.74 (Table 2). However, this is not that much higher than several of the sites across native ranges; albeit they did vary widely. The diversity scores were not linearly associated with latitudinal or longitudinal gradients (Table 2), thus I am confident this increase in dietary diversity is a result of feeding strategy, rather than the result of some prey species assemblage cline (Hillebrand, 2004).

Table 1. Outcomes of Chi-squared testing between diet makeup of native and invasive ranges of Eastern Red-backed Salamanders, *Plethodon cinereus*. Presented are prey item categories, the proportion that prey made up within the diet of the native and invasive range, as well as the standardized number (n) and the test statistics (x^2). Bold values indicate significance.

Prey Item	**Proportion within Native**	**Proportion within Invasive**	***n***	**x^2, *p* =**
Acari	0.29470	0.17521	46991	**< 0.01**
Annelida	0.01048	0.02796	3844	**< 0.01**
Araneae	0.01750	0.03728	5478	**< 0.01**
Archaeognatha	0.00005	0.00000	5	**< 0.01**
Coleoptera	0.05585	0.10065	15651	**< 0.01**
Collembola	0.20696	0.21622	42318	**< 0.01**
Dermaptera	0.00005	0.00000	5	**< 0.01**
Diplura	0.00005	0.00000	5	**< 0.01**
Diptera	0.04745	0.02982	7727	**< 0.01**
Gastropoda	0.03129	0.02237	5366	**< 0.01**
Hemiptera	0.00405	0.00839	1244	**< 0.01**
Homoptera	0.00015	0.00000	15	**< 0.01**
Hymenoptera	0.05363	0.00932	6295	**< 0.01**
Hymenoptera_Formicidae	0.08724	0.00652	9377	**< 0.01**
Insecta_Unknown	0.05304	0.01864	7168	**< 0.01**
Isopoda	0.07370	0.15564	22934	**< 0.01**
Ixodida	0.00035	0.00466	501	**< 0.01**
Lepidoptera	0.00593	0.00093	686	**< 0.01**
Myriapoda	0.02615	0.14632	17247	**< 0.01**
Nematoda	0.00015	0.00000	15	**< 0.01**
Opiliones	0.00203	0.01678	1880	**< 0.01**
Orthoptera	0.00020	0.00000	20	**< 0.01**
Plecoptera	0.00025	0.00000	25	**< 0.01**
Plethodon_cinereus	0.00005	0.00000	5	**< 0.01**
Protura	0.00099	0.00000	99	**< 0.01**
Pseudoscorpionida	0.01018	0.00000	1018	**< 0.01**
Psocoptera	0.00657	0.00000	657	**< 0.01**
Symphyla	0.00000	0.00466	466	**< 0.01**
Thysanoptera	0.00069	0.00000	69	**< 0.01**
Trichoptera	0.00005	0.00000	5	**< 0.01**
Turbellaria	0.00005	0.00000	5	**< 0.01**
Unknown	0.01018	0.01864	2882	**< 0.01**

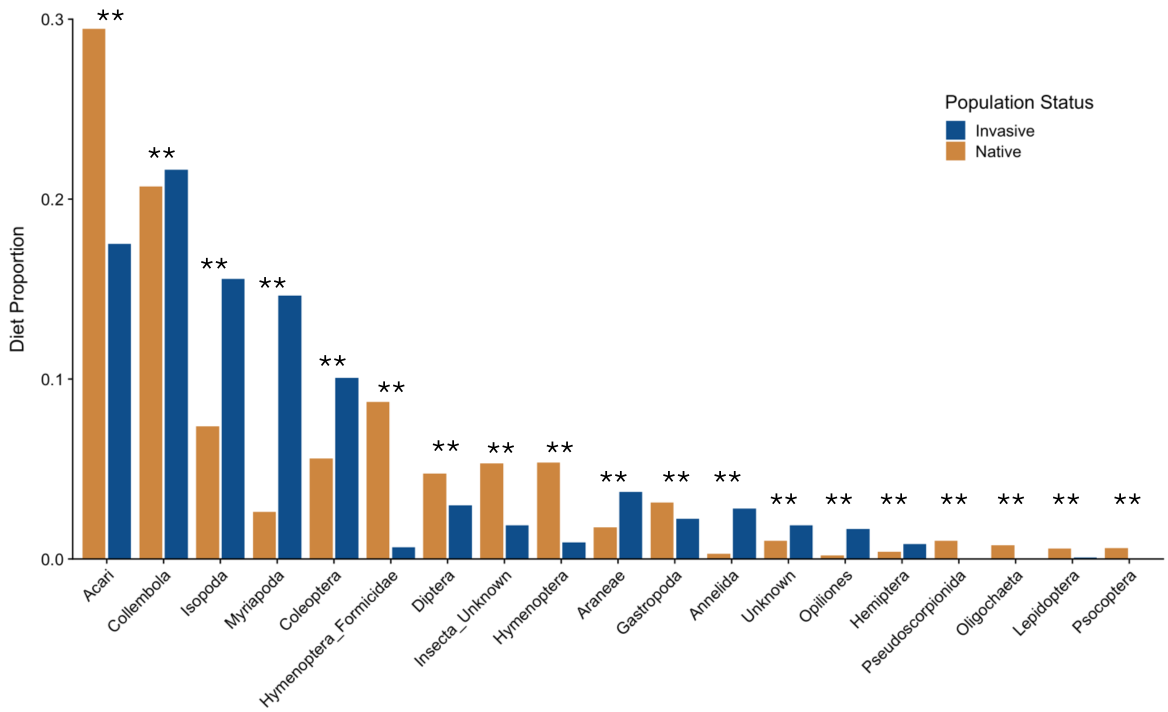

Figure 2. Diet proportion of top 19 prey items found in Eastern Red-backed Salamander, *Plethodon cinereus,* in native populations (n = 1318) through systematic literature review (brown bars) and invasive population (n = 133) through dissections (blue bars). Significance calculated with Chi-Square. Significance ($p < 0.001$) is denoted by two asterisks (**).

Dietary Composition of the Invasive Population

The dissected salamanders from my study had a vacuity index of 3.0% with only 4 empty stomachs out of 133 salamanders.

Of those that contained prey items (n = 129), the diet items that made up more than 10% in the salamanders' diet in abundance were Isopoda (15.56%), Entomobryomorpha (13.89%), Mesostigmata (12.86), and Coleoptera (10.07%). By volume the prey items that composed over 10 percent of my study's salamanders' diet were Isopoda (19.45%), Lumbricidae (15.94%), Coleoptera (12.49%), Geophilomorpha (11.87%), and Lithiomorpha (11.15%) (Table 3).

From the Chi-Squared analysis there is a statistically higher count of native prey in their diet with 63.8% of the diet being native prey and 36.2% comprising of invasive prey (x^2_1 = 82.208, $p < 0.001$) (Figure 3). Using a Wilcoxon ranked sum test the volume of invasive prey items within the Newfoundland salamanders' diet is statistically higher than the volume of native prey (W = 55348, $p < 0.001$) (Figure 4). By volume the invasive prey items accounted for 67% and the native prey items accounted for 33%.

Table 2. Locations from study sites with their latitude and longitude coordinates and corresponding Shannon-Wiener diversity index. Bolded values indicate invasive Newfoundland population.

Latitude	Longitude	Shannon Wiener Index
36.228972	-82.36125	1.62
37.523611	-79.506111	2.15
37.651972	-77.658333	1.98
40.129111	-79.1915	0.29
41.229617	-81.518825	2.59
41.234083	-81.5005	0.49
41.286667	-81.571833	2.07
41.343528	-82.4875	2.18
41.4545	-81.329722	1.60
41.492694	-81.592667	1.87
43.032444	-76.137556	1.39
43.16018	-73.09677	2.03
43.36733	-72.9128	2.11
43.92779	-71.38683	2.39
43.92865	-71.39465	2.08
43.97367	-71.18802	1.94
43.98785	-71.90552	2.73
44.09015	-73.05123	2.14
45.404444	-71.888333	2.17
47.48575	**-52.97525**	**2.74**

Table 3. Prey items identified through dissection of the stomachs of invasive *Plethodon cinereus* (n = 133). Prey items identified by class and order. For each prey group I present the count (n), proportion by count, proportion (%n), percent native prey (%N), percent invasive prey (%I), the total volume in mm^3 (Total V), and the percent of volume compared to the whole diet (V%). Bolded volume percent indicate volume over 10% of total diet.

Class	Order	*n*	% n	% N	% I	Total V	V (%)
Arachnida	Araneae	38	3.54	58	42	31.12	0.83
	Ixodida	5	0.47	100	0	1.61	0.04
	Mesostigmata	138	**12.86**	100	0	33.94	0.91
	Opiliones	18	1.68	100	0	76.41	2.05
	Oribatida	1	0.09	100	0	0.06	0.00
	Sarcoptiformes	47	4.38	100	0	7.87	0.21
	Trombidiformes	2	0.19	100	0	0.64	0.02
	Unknown	2	0.19	100	0	0.40	0.01
Arthropod	Unknown	8	0.75	100	0	47.27	1.27
Chilopoda	Geophilomorpha	24	2.24	0	100	443.08	**11.87**
	Lithobiomorpha	89	8.29	0	100	416.24	**11.15**
Clitellata	Enchytraeida	9	0.84	100	0	17.60	0.47
	Lumbricidae	21	1.96	0	100	594.70	**15.94**
Diplopoda	Julida	13	1.21	0	100	34.83	0.93
	Polydesmida	31	2.89	0	100	147.59	3.96
Entognatha	Entomobryomorpha	149	**13.89**	100	0	58.68	1.57
	Mesostigmata	1	0.09	100	0	0.15	0.00
	Poduromorph	14	1.30	100	0	3.28	0.09
	Symphypleona	66	6.15	100	0	12.54	0.34
	Unknown	2	0.19	100	0	0.43	0.01
Gastropoda	Stylommatophora	22	2.05	95	5	83.34	2.23
	Unknown	2	0.19	100	0	21.72	0.58
Insecta	Coleoptera	108	**10.07**	72	28	465.93	**12.49**
	Diptera	32	2.98	100	0	97.51	2.61
	Hemiptera	9	0.84	100	0	63.76	1.71
	Hymenoptera	17	1.58	100	0	29.31	0.79
	Lepidoptera	1	0.09	100	0	24.51	0.66
	Unknown	20	1.86	100	0	24.56	0.66
Malacostraca	Isopoda	167	**15.56**	2	98	725.68	**19.45**
Symphyla	Scolopendrellida	5	0.47	100	0	6.89	0.18
Unknown	Unknown	12	1.12	100	0	259.90	6.97

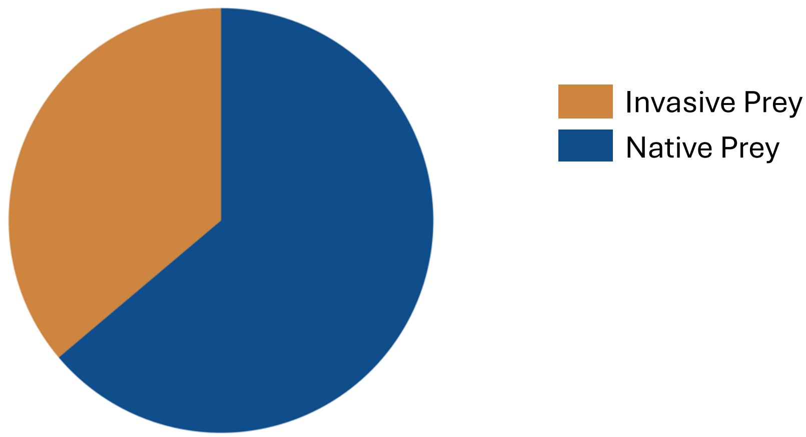

Figure 3. Percent invasive and native prey found in the diet of Newfoundland salamander population. Invasive prey = 37%, native prey = 63%, (x^2_1 = 82.208, $p < 0.001$).

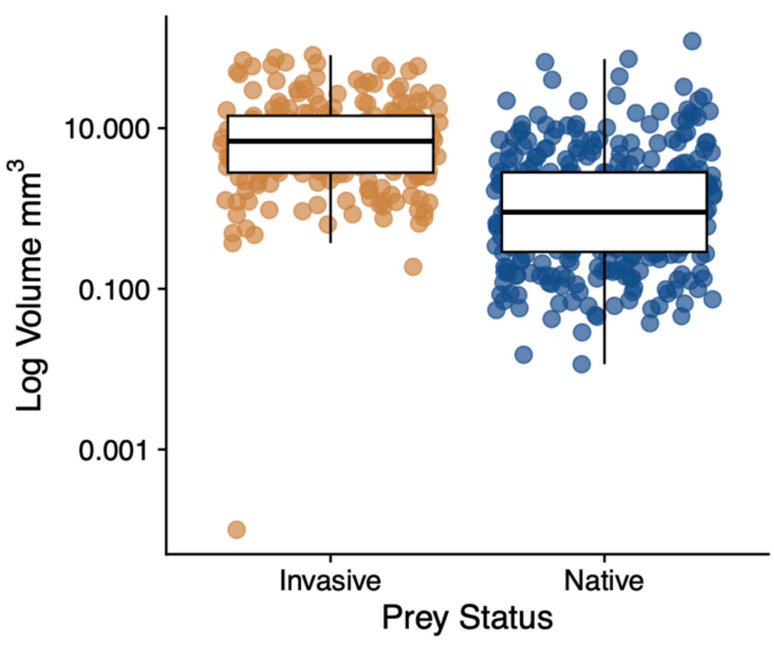

Figure 4. Volume of invasive and native prey found within the diet of each Newfoundland salamander (W = 55348, $p < 0.001$). Brown points are for invasive prey items, blue points are for native prey items. Y axis is on a log scale.

Discussion

My study provides support for the idea that the success of the invasive population of Eastern Red-backed Salamanders, *Plethodon cinereus*, in Newfoundland can be attributed to their ability to exploit niche opportunities by altering their diet and exploiting pre-existing invasive prey communities. I found that there were strong dietary shifts when comparing the Newfoundland population to native populations – aligning with the Dietary Niche Increase hypothesis (Vazquez, 2006) and Dietary Plasticity hypothesis (Richards et al., 2006). Additionally, this invasive salamander population relies heavily on invasive prey items both in count and volume to make up a large proportion of their diet, providing support for the Invasion Meltdown hypothesis (Simberloff and Holle 1999).

One of the leading ways that invasive populations can become established is related to their ability to capitalize on novel resources and leverage a generalist diet (Peterson & Vieglais, 2001; Marvier et al., 2004; David et al., 2017). In novel environments this is particularly important as the prey items that were previously relied upon may not be available or at lower proportions when compared to their native habitats. If an invading population can capitalise on a wider variety of resources or if they are able to shift to use underexploited prey types, then they can better integrate into a novel environment and allocate more energy into reproduction and population growth (i.e., Niche Breadth Invasion Success hypothesis; Vazquez, 2006). This is exactly what I observed within the diets of the invasive Eastern Red-backed Salamander population in Newfoundland. Within their gut contents, I determined that compared to native populations they changed their diet proportions (Table 1); shifting away from feeding heavily on Acari (mites) and instead feeding more heavily on a wider variety of prey. In total, the invasive Newfoundland salamander population eats significantly more Collembola (springtails), Isopoda (wood lice), Myriapoda (centipedes and millipedes), Coleoptera (beetles), Araneae (spiders), Annelida (earth worms), Opiliones (harvestmen), and Hemiptera (true bugs) than the native population (Figure 2). Meanwhile, this invasive population shows a significant decrease in the amount of Acari (mites), Hymenoptera: Formicidae (ants), Diptera (flies), Hymenoptera (bees and wasps; other than ants), Gastropoda (slugs and snails), Pseudoscorpionida (pseudoscorpions), Lepidoptera (butterflies and moths), and Pscoptera (booklice) than native populations. Based on the combined diet of salamanders from the native range, I found that 16 of the 32 prey groups found within the diet of the native salamander population were not found within the invasive salamander population; these groups included: Dermaptera (earwigs), Diplura (two-pronged bristletails), Homopotera (aphids), Nematoda (round worms), Orthoptera (grasshoppers and crickets), Plecoptera (stoneflies), Protura (coneheads), Pseudoscorpionida (false scorpions), Pscoptera (other bark lice), Thysanoptera (thrips), Trichoptera (caddisflies), Turbellaria (flatworms), and conspecific (one account of cannibalism in native population (Maerz, 2003). However, most of these prey groups only made-up small proportions of the overall diet. In fact, the changes in the proportion of major prey items seen in the invasive population, when compared to each of the native populations examined (n = 20), are likely the driver of the slight increase in the biodiversity score (i.e., Shannon-Weiner Diversity index score; see Table 2). This increase in prey diversity is likely due to more evenness in the proportion of prey types within the invasive salamander population's diet, due to them moving away from an Acari-heavy diet, to one that incorporated a much higher proportion of Isopoda, Myriapoda, and Coleoptera. The shift to an invasive diet higher in proportion of Isopoda, Myriapoda, and Coleoptera has previously been seen in other invasive amphibian populations on islands (Beard 2007; Baxter-Gilbert et al. 2020). For example, the invasive population of Guttural Toads (*Sclerophrys gutturalis*) in Mauritius significantly increased the portion of isopods consumed compared to native populations (Baxter-Gilbert et al. 2020; Peta 2022) and the invasive Coquí Frog(*Eleutherodactylus coqui*) population in Hawai'i was found to have a high prey preference towards isopods, coleoptera and myriapods (Beard, 2007). With respect to the invasive salamanders of Newfoundland, these changes in prey composition could signify: (1) a trade-off for more energetically favourable foods by the invasive population, (2) there are less available Acari in Newfoundland, or (3) there is less local competition for Isopoda, Myriapoda, and Coleoptera prey and thus these groups represent an available resource that could be more easily exploited by the invading salamanders. I recommend future research examine aspects of prey preferences and local invertebrate community composition to determine which driver is causing the dietary shift I have observed.

My findings that the invasive salamander population may have increased their ability to succeed in proliferating in Newfoundland by expanding their dietary niche and strong dietary plasticity, follows what has been previously observed in several other invasive species, though it is not a ubiquitous trend. For example, this dietary niche broadening has been seen in the African Clawed Frog when comparing its diet in the invasive range in France to its native South African range (Courant et al., 2017). Similar shifts can be seen in the dietary plasticity and ability to easily adjust dietary niche breadth of invasive rat (*Rattus* sp.) populations on small islands around New Caledonia, whereby when primary food sources (e.g., seabird eggs and chicks) are depleted, the rats immediately transition to exploit hatchling sea turtles (Caut et al., 2008). This remarkable ability to flexibly shift dietary preferences underscores not only the adaptability and resilience of invasive species but the harm they can cause to a wide range of native taxa, including endangered species (Caut et al., 2008). Niche breadth increases has also been hypothesised as a mechanism that can allow species to adapt to urban environments (Palacio, 2020) – another form of novel landscape/ecosystem colonisation. For example, bird species that have a broader dietary niche have a pronounced propensity to better exploit the urban landscape (Palacio, 2020). With increased urbanisation and globalization driving an uptick in invasive species in human modified environments, understanding the dietary dynamics facilitating their proliferation becomes increasingly important (Hudgins et al., 2022; Seebens et al., 2017). However, niche widening may not always be the mechanism taken by an invasive species. The American Bullfrog is a generalist species native to North America which now has a worldwide invasive range, yet when invading, this species has a significantly truncated niche breadth compared to that of its native range (Bissattini & Vignoli, 2017). This is due to the species shifting to specialise on the most abundant prey present, thus focusing their trophic strategy, and decreasing their niche breath (Bissattini & Vignoli, 2017). This adaptability enables the bullfrog to capitalize on prevailing ecological conditions, facilitating its invasion and establishment in diverse habitats worldwide.

My findings also demonstrated that the shift in diet composition showed a high proportion of invasive prey (36.2%), suggesting that the previously established invasive invertebrate community may have facilitated the successful establishment of this salamander in Newfoundland. This was further underscored when I accounted for biomass, with 67% of the volume of prey being represented by invasive invertebrates (Figure 4). As such, a majority of the biomass consumed by the salamanders in Newfoundland is coming from prey that similarly has not evolved in the ecosystem and may be underexploited in the region due to the potential absence of their evolved predators (Keane & Crawley, 2002). This finding directly aligns with the concept behind the Invasional Meltdown Hypothesis (Simberloff and Holle 1999), suggesting the previous invasions of invertebrates to Newfoundland created an open niche, or at least increased niche opportunities, for invading Eastern Red-back Salamanders to capitalise upon. This is similar to what was seen in the Zhoushan Archipelago in China where a study found that invasive American Bullfrog populations preferentially preyed on invasive crayfish - which actually lessened the frog's negative impact on the native prey community (Liu et al., 2018). Similarly, the Coquí Frog that invaded Hawai'i, was found to have a large proportion of their diet (by volume) comprised of invasive termites and ants (Beard, 2007). In general, these studies, as well as my own presented here, demonstrate a means by which invasive predators are able to integrate into ecosystems within which the evolved niche of the invader may already be fully exploited by native taxa, and thus a modified one is required for invasion success (Simberloff and Holle 1999). In other words, the presence of pre-existing invasive prey creates novel niche opportunities for the incoming invader to capitalise on. This also means that anthropogenic activities that promote the spread and establishment of some invasive species, including some that many may consider benign (e.g., isopods), can have knock-on effects that promote the invasive potential for other taxa that might be seen as more ecologically or economically hazardous (e.g., invasive amphibians).

At the core of all biological invasions is human activity, both in the spread of invasives species (Seebens et al. 2017), as well as the disturbance of natural areas and disrupted ecological processes that create niche opportunities (Jeschke and Strayer 2006). Furthermore, research has identified that urbanization and other human influences can lead to an increase in the invasive invertebrate populations within these areas (Hudgins et al., 2022). In this context of the successful establishment of Eastern Red-back Salamanders in Newfoundland which is bolstered by Invasional Meltdown hypotheses mechanisms (i.e., a large and diverse invasive invertebrate community), the salamander population success may be secondarily promoted by anthropologically disturbed areas promoting invasive prey. This postulate is supported by the fact that all of the individual salamanders used in my study were collected from suburban backyards and within debris piles around human settlements. Furthermore, the researchers that undertook the field collections reported surveying natural habitats (e.g., forests, upland habitat with cover objects, and wetland patches), but finding no salamanders in these areas; these invasive salamanders were only seen within anthropogenically disturbed habitats (J. Baxter-Gilbert *pers comm*.). This observation, coupled with my findings (presented here), illustrate the multifaceted means by which human activity has bettered the odds for these salamanders to overcome the ecological barriers that otherwise might have prevented their invasion.

Overall, my results show us that the diet of Eastern Red-backed Salamanders in Newfoundland differs from the general diet of conspecific populations across their native range and that the invaders rely heavily on invasive invertebrates. Unfortunately, there is little known about the specifics of invasive invertebrate communities in Newfoundland (e.g., density, abundance, invasion history, and ecological role and impact). Therefore, further research is warranted to address these gaps and expand our knowledge in four key areas. Firstly, comprehensive studies of the current invertebrate communities in Newfoundland are essential to gain a better understanding of the available prey items for salamanders. This could be achieved through methodologies such as pitfall trapping or leaf litter sampling, allowing for a more nuanced assessment of prey availability (Beard, 2007; Courant et al., 2017). Secondly, use information on prey availability and diet composition to calculate a Relativized Electivity Index to examine the salamanders' dietary choices in relation to the abundance and nutritional value of available prey items (Baxter-Gilbert et al., 2021; Peta 2022). This approach would shed light on whether salamanders are actively selecting larger, more nutrient-dense invasive prey or simply consuming them due to their higher abundance and frequent encounter rates. Thirdly, investigating nutritional shifts in prey items, such as comparing the caloric content of Acari versus Isopoda, Myriapoda, and Coleoptera could elucidate the drivers behind dietary changes observed in invasive salamander populations. Lastly, work on this population should examine the genetics of the Newfoundland population to determine the source population(s), the genetic structure, and health of the population. Work should be done to examine the spread of the species on the island and determine how far the invasion has progressed and if populations are present outside of Conception Bay South.

Invasive species are one of the largest threats to biodiversity in our changing world (Seebens et al., 2017). Although most of the biomass of this invasive salamander population's diet is coming from invasive prey items, a substantial proportion is also native species. This may be a sign that Eastern Red-backed Salamanders pose a threat to the ecosystem in Newfoundland. Small invertebrate species such as Acari (mites) and Entognatha (springtails) that are native in Newfoundland are very important to the ecosystem, as they play important roles in organic decomposition, nutrient cycling, mineralising plant nutrients, and play important roles in above ground food webs (Behan-Pelletier, 1999; Johnston, 2000; Elmoghazy & Shawer, 2013). Although the invasive salamander population is eating a large amount of Acari (n = 206), these oribatid mites often number between 250,000 to 500,000/m^2 (Coleman et al., 2017). Therefore, there is likely not a large impact on the native microarthropod community – at least not from the densities of invasive salamanders that are currently being observed. Yet, if this invasive salamander population's density continues to grow, this may change. Nevertheless, understanding the dietary preferences of a newly described invasive species and their utilization of previously established non-native prey allows us to underscore the broader theoretical implications to invasion biology. By recognizing the pivotal role of previously established invasive invertebrates in Newfoundland, my study highlights how their proliferation creates open niches for new predator taxa, like Eastern Red-backed Salamanders, to thrive. This is pertinent, as invasive invertebrates make up one of the largest proportions of invasive taxa around the globe, second only to plants, due to their small size, easy '*hitchhiking*' abilities, and relatively rapid reproductive rates (Pimentel et al., 2005; Padayachee et al., 2017). Due to the increasing numbers of invasive invertebrates around the world, and the ability for generalist vertebrate predators, like Eastern Red-backed Salamanders, to feed on them, we may expect to see even more invasive species continue to spread and invade; as they are able to use previously established invertebrate prey communities as a springboard to strengthen their invasive potential.

In conclusion, my study sheds valuable light on the intricate interplay between invasive species and their dietary preferences, and how this can relate to invasion success. I found that the established invasive population of Eastern Red-backed Salamanders in Newfoundland, Canada, had shifted their diet, when compared to native conspecifics, by both increasing the diversity of their prey items and shifting to a more generalised diet (supporting the Niche Breadth Invasion Success hypothesis; Vazquez, 2006). My findings also align with a second established invasion theory, the Invasional Meltdown Hypothesis, as a large proportion of the biomass being consumed by the salamanders consisted of invasive invertebrates illustrating how the proliferation of invasive species can create open niches and facilitate the invasion of other taxa (Simberloff and Holle 1999). Moreover, this study highlights the adaptability and resilience of invasive species, as they capitalize on novel resources and exhibit dietary plasticity to thrive in new environments (David et al., 2017). Understanding the dietary dynamics of invasive species provides crucial insights into the mechanisms driving invasion success and ecosystem disruptions (Seebens et al., 2017). By examining invasions and breaking down the intricate interactions between invasive species and their prey, we can better predict and manage invasive species' impacts on native ecosystems and understand the mechanisms that facilitated the invasion.

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Supplementary materials

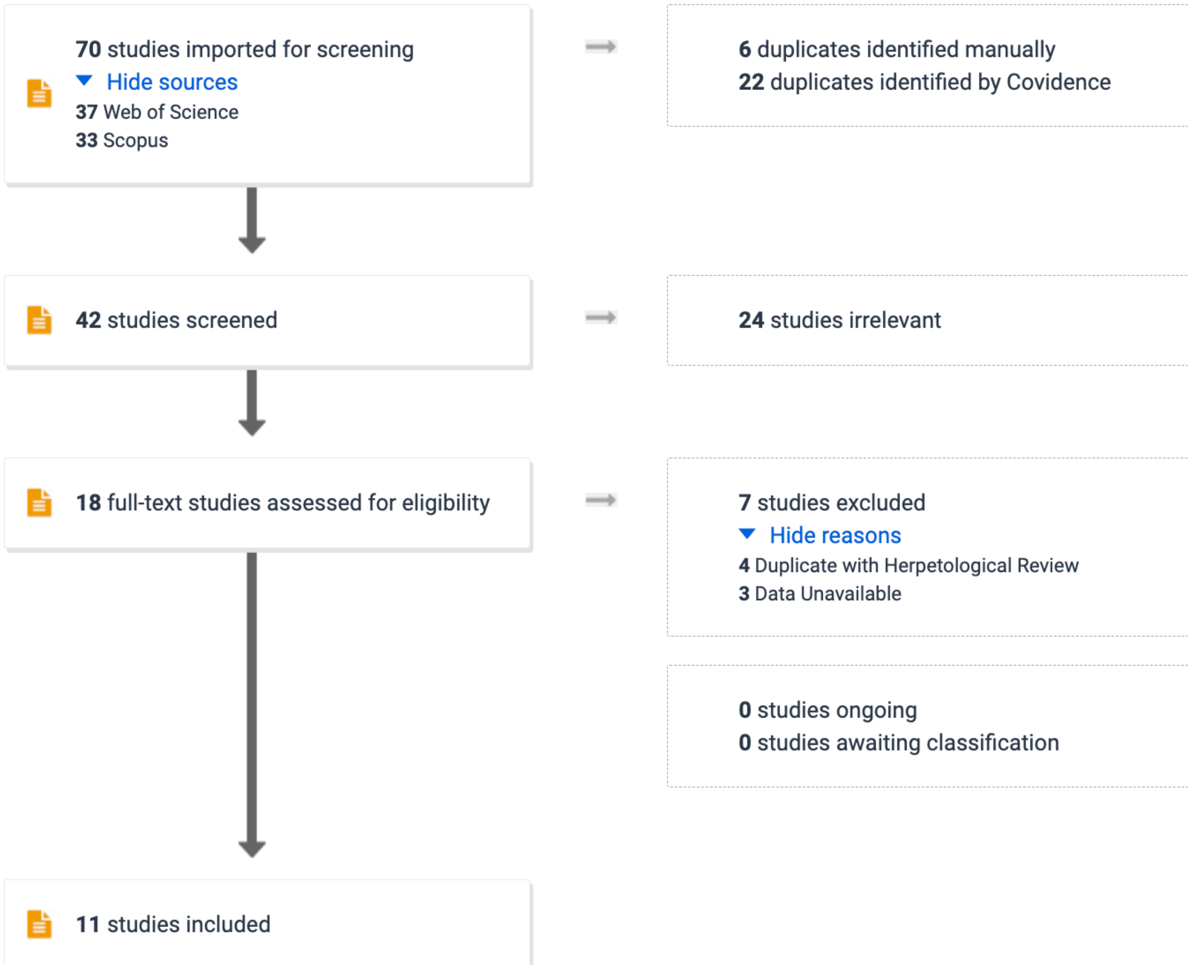
SM Table 1. Prey items identified through dissection of the stomachs of *Plethodon cinereus* (*n* = 133). Prey items identified by class, order, family, genus, and species where possible. For each prey group I present the count (*n*), proportion by count, percent native prey (%N), percent invasive prey (%I), and the percent of volume compared to the whole diet (V%).

Class	Order	Family	*Genus*	*Species*	*n*	%N	%I	%V
Arachnida	Araneae	Clubionidae			1	100	0	0.007
Arachnida	Araneae	Linyphiidae	*Pityohyphantes*		2	100	0	0.021
Arachnida	Araneae	Linyphiidae	*Tenuiphantes*		1	100	0	0.009
Arachnida	Araneae	Linyphiidae			6	100	0	0.103
Arachnida	Araneae	Miturgidae	*Chiracanthium*	*iclusum*	1	100	0	0.004
Arachnida	Araneae	Pholcidae			10	0	100	0.227
Arachnida	Araneae	Theridiidae	*Enoplognatha*	*ovata*	6	0	100	0.178
Arachnida	Araneae	Unknown			11	100	0	0.286
Arachnida	Ixodida	Ixodidae	*Haemaphysalis*	*leporispalustris*	2	100	0	0.013
Arachnida	Ixodida	Ixodidae			1	100	0	0.009
Arachnida	Ixodida				2	100	0	0.021
Arachnida	Mesostigmata				138	100	0	0.909
Arachnida	Opiliones	Nemastomatidae	*Nemastoma*	*lugubre*	3	100	0	0.186
Arachnida	Opiliones	Phalangiidae	*Oligolophus*	*hansenii*	2	100	0	0.191
Arachnida	Opiliones	Phalangiidae	*Phalangium*	*opilio*	1	100	0	0.040
Arachnida	Opiliones	Phalangiidae	*Rilaena*	*triangularis*	2	100	0	0.469
Arachnida	Opiliones	Phalangiidae	*Rilaena*	*triangularis*	1	100	0	0.366
Arachnida	Opiliones	Phalangiidae			9	100	0	0.796
Arachnida	Oribatida				1	100	0	0.002
Arachnida	Sarcoptiformes				47	100	0	0.211
Arachnida	Trombidiformes				2	100	0	0.017
Arachnida	Unknown				2	100	0	0.011
Arthropod	Unknown				8	100	0	1.267

Chilopoda	Geophilomorpha	Himantariidae	*Haplophilus*	*subterraneus*	3	0	100	0.584
Chilopoda	Geophilomorpha	Himantariidae	*Haplophilus*	*subterraneus*	19	0	100	9.942
Chilopoda	Geophilomorpha	Himantariidae			2	0	100	1.348
Chilopoda	Lithobiomorpha	Lithobiidae	*Lithobius*	*forficatus*	84	0	100	10.937
Chilopoda	Lithobiomorpha	Lithobiidae	*Lithobius*	*microps*	2	0	100	0.069
Chilopoda	Lithobiomorpha	Lithobiidae			2	0	100	0.060
Chilopoda	Lithobiomorpha				1	0	100	0.088
Clitellata	Enchytraeida	Enchytraeidae			9	100	0	0.472
Clitellata	Lumbricidae	Lumbricidae	*Lumbricus*	*terrestris*	21	0	100	15.937
Diplopoda	Julida	Blaniulidae			8	0	100	0.427
Diplopoda	Julida	Julidae	*Brachyiulus*		3	0	100	0.362
Diplopoda	Julida	Julidae	*Cylindroiulus*	*punctatus*	2	0	100	0.145
Diplopoda	Polydesmida	Polydesmidae	*Polydesmus*	*angustus*	16	0	100	2.496
Diplopoda	Polydesmida	Polydesmidae	*Polydesmus*		1	0	100	0.060
Diplopoda	Polydesmida	Polydesmidae			14	0	100	1.399
Entognatha	Entomobryomorpha	Entomobryidae	*Entomobrya*	*nivalis*	1	100	0	0.069
Entognatha	Entomobryomorpha				148	100	0	1.504
Entognatha	Mesostigmata				1	100	0	0.004
Entognatha	Poduromorph	Hypogastruridae			1	100	0	0.004
Entognatha	Poduromorph	Neanuridae			8	100	0	0.052
Entognatha	Poduromorph				5	100	0	0.032
Entognatha	Symphypleona	Arthopalitidae			1	100	0	0.001
Entognatha	Symphypleona	Dicyrtomidae			51	100	0	0.267
Entognatha	Symphypleona	Dicyrtomidae	*Dicyrtoma*	*flammea*	2	100	0	0.020
Entognatha	Symphypleona	Sminthurididae			1	100	0	0.018
Entognatha	Symphypleona				11	100	0	0.030
Entognatha	Unknown				2	100	0	0.011
Gastropoda	Stylommatophora	Agriolimacidae			1	100	0	0.455
Gastropoda	Stylommatophora	Gastrodontidae	*Perpolita*		4	100	0	0.322

Gastropoda	Stylommatophora	Hygromiidae	*Trochulus*	*hispidus*	1	0	100	0.057
Gastropoda	Stylommatophora	Vitrinidae	*Vitrina*		3	100	0	0.241
Gastropoda	Stylommatophora	Vitrinidae			1	100	0	0.022
Gastropoda	Stylommatophora				12	100	0	1.136
Gastropoda	Unknown				2	100	0	0.582
Insecta	Coleoptera	Carabidae	*Clivina*	*fossor*	1	0	100	0.103
Insecta	Coleoptera	Carabidae	*Harpalus*	*rufipes*	2	0	100	0.516
Insecta	Coleoptera	Carabidae	*Pterostichus*		2	100	0	1.056
Insecta	Coleoptera	Chrysomelidae	*Chrysolina*	*hyperici*	1	0	100	0.032
Insecta	Coleoptera	Chrysomelidae			3	0	100	0.090
Insecta	Coleoptera	Cryptophagidae	*Cryptophagus*		2	100	0	0.133
Insecta	Coleoptera	Curculionidae	*Barypeithes*	*pellucidus*	3	0	100	0.355
Insecta	Coleoptera	Curculionidae	*Dendroctonus*		1	100	0	0.076
Insecta	Coleoptera	Curculionidae	*Glocianus*		1	0	100	0.117
Insecta	Coleoptera	Curculionidae	*Hypera*	*nigrirostris*	2	0	100	0.424
Insecta	Coleoptera	Curculionidae	*Isochnus*	*sequensi*	1	0	100	0.035
Insecta	Coleoptera	Curculionidae	*Orthochaetes*	*setiger*	1	0	100	0.038
Insecta	Coleoptera	Curculionidae	*Otiorhynchus*	*porcatus*	1	0	100	0.596
Insecta	Coleoptera	Curculionidae	*Phyllobius*	*oblongus*	5	0	100	0.737
Insecta	Coleoptera	Curculionidae	*Phyllobius*	*oblongus*	2	0	100	0.149
Insecta	Coleoptera	Curculionidae	*Sitona*	*hispidulus*	2	0	100	0.174
Insecta	Coleoptera	Curculionidae	*Tychius*		2	0	100	0.090
Insecta	Coleoptera	Curculionidae			5	100	0	0.580
Insecta	Coleoptera	Elateridae	*Agriotes*	*ineatus*	1	0	100	0.169
Insecta	Coleoptera	Elateridae	*Agriotes*	*mancus*	1	0	100	0.804
Insecta	Coleoptera	Hydrophilidae	*Anacaena*	*limbata*	1	0	100	0.077
Insecta	Coleoptera	Latridiidae			3	100	0	0.014
Insecta	Coleoptera	Staphylinidae	*Palporus*	*nitidulus*	5	100	0	0.099
Insecta	Coleoptera	Staphylinidae	*Stenus*		2	100	0	0.074

Insecta	Coleoptera	Staphylinidae			44	100	0	5.586
Insecta	Coleoptera				14	100	0	0.361
Insecta	Diptera	Anisopodidae	*Sylvicola*	*fenestralis*	2	100	0	0.049
Insecta	Diptera	Calliphoridae	*Calliphora*		1	100	0	0.083
Insecta	Diptera	Calliphoridae			1	100	0	0.077
Insecta	Diptera	Culicidae			1	100	0	0.003
Insecta	Diptera	Cyclorrhapha			1	100	0	1.947
Insecta	Diptera	Phoridae			4	100	0	0.111
Insecta	Diptera	Sciaridae			21	100	0	0.307
Insecta	Diptera	Sphaeroceridae			1	100	0	0.037
Insecta	Hemiptera	Rhyparochromidae	*Drymus*	*unus*	6	100	0	1.073
Insecta	Hemiptera	Rhyparochromidae			2	100	0	0.458
Insecta	Hemiptera				1	100	0	0.177
Insecta	Hymenoptera	Chrysidoidea			1	100	0	0.007
Insecta	Hymenoptera	Fanniidae			1	100	0	0.011
Insecta	Hymenoptera	Formicidae	*Formica*	*glacialis*	1	100	0	0.161
Insecta	Hymenoptera	Formicidae	*Myrmica*	*detritinodis*	6	100	0	0.431
Insecta	Hymenoptera	Pergidae	*Acordulecera*	*dorsalis*	1	100	0	0.151
Insecta	Hymenoptera	Tenthredinidae			1	100	0	0.003
Insecta	Hymenoptera				6	100	0	0.021
Insecta	Lepidoptera	Noctuidae	*Nephelodes*	*minians*	1	100	0	0.657
Insecta	Unknown				20	100	0	0.658
Malacostraca	Isopoda	Porcellionidae	*Porcellio*	*scaber*	161	0	100	18.679
Malacostraca	Isopoda	Porcellionidae			2	0	100	0.110
Malacostraca	Isopoda	Trichoniscidae	*Trichoniscus*	*pusillus*	2	100	0	0.421
Malacostraca	Isopoda				2	100	0	0.237
Symphyla	Scolopendrellida	Scutigerellidae	*Scutigerella*		5	100	0	0.185
Unknown	Unknown				12	100	0	6.965



SM Figure 1. PRISMA diagram for data extraction to examine native range dietary niche breadth of Eastern Red-back Salamanders.

SM Table 2. Sources from which data was extracted to examine native range dietary niche breadth of Eastern Red-back Salamanders. Citation, location, and number of salamanders (S (*n*)) for each article.

Citation	**Location**	**S (*n*)**
Anthony, C. D., Venesky, M. D., & Hickerson, C. A. M. (2008). Ecological separation in a polymorphic terrestrial salamander. *Journal of Animal Ecology*, *77*(4), 646-653.	Ohio	81
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