




RESEARCH ARTICLE

Resource competition drives an invasion-replacement event among shrew species on an island

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Abstract

1. Invasive mammals are responsible for the majority of native species extinctions on islands. While most of these extinction events will be due to novel interactions between species (e.g. exotic predators and naive prey), it is more unusual to find incidences where a newly invasive species causes the decline/extinction of a native species on an island when they normally coexist elsewhere in their overlapping mainland ranges.
2. We investigated if resource competition between two insectivorous small mammals was playing a significant role in the rapid replacement of the native pygmy shrew *Sorex minutus* in the presence of the recently invading greater white-toothed shrew *Crocidura russula* on the island of Ireland.
3. We used DNA metabarcoding of gut contents from >300 individuals of both species to determine each species' diet and measured the body size (weight and length) during different stages of the invasion in Ireland (before, during and after the species come into contact with one another) and on a French island where both species have long coexisted (acting as a natural 'control' site). Dietary composition, niche width and overlap and body size were compared in these different stages.
4. The body size of the invasive *C. russula* and composition of its diet changes between when it first invades an area and after it becomes established. During the initial stages of the invasion, individual shrews are larger and consume larger sized invertebrate prey species. During later stages of the invasion, *C. russula* switches to consuming smaller prey taxa that are more essential for the native species. As a result, the level of interspecific dietary overlap increases from

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between 11% and 14% when they first come into contact with each other to between 39% and 46% after the invasion.

- Here we show that an invasive species can quickly alter its dietary niche in a new environment, ultimately causing the replacement of a native species. In addition, the invasive shrew could also be potentially exhausting local resources of larger invertebrate species. These subsequent changes in terrestrial invertebrate communities could have severe impacts further downstream on ecosystem functioning and services.

KEYWORDS

diet, DNA metabarcoding, invasive species, invertebrates, Ireland, mammal, niche overlap

1 | INTRODUCTION

The rate at which species are introduced into novel, non-native ranges has been accelerating due to increased globalisation (Hulme, 2009; Seebens et al., 2017). As well as increasing societal impacts associated with the management costs of these invasions (Diagne et al., 2021), the ecological impacts that newly introduced invasive species can have on local ecosystems are now so severe that they are considered the most common cause of vertebrate extinctions (Bellard, Cassey, et al., 2016). This is particularly evident in island ecosystems, where invasive species are responsible for most of the damage/impacts caused to local fauna and flora (Bellard, Cassey, et al., 2016; Bellard, Genovesi, et al., 2016; Spatz et al., 2017). Islands often have more simplified ecological systems with smaller species communities than their mainland counterparts and therefore tend to be more susceptible to anthropogenic impacts (Spatz et al., 2017). Invasive species have been implicated in >80% of species extinctions on islands over the last 500 years (Bellard, Cassey, et al., 2016), and invasive mammals are responsible for the majority of these extinctions (Jones et al., 2016).

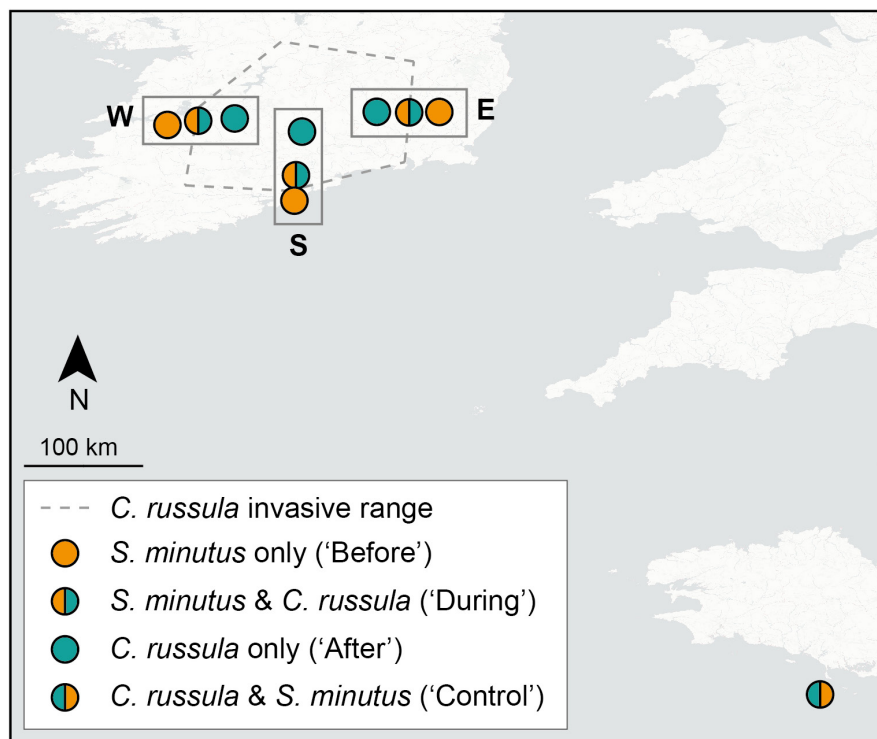
The impacts of species invasions can either be through direct (e.g. predation; Doherty et al., 2016) or indirect (e.g. competition or trophic cascades; Hernandez-Brito et al., 2018; Benkwitt et al., 2021) mechanisms. The strength of any competitive interaction between invasive and native species may depend on the community composition and environment of the invaded area, the speed of the invasion and potential trade-offs between dispersal, reproduction and competitive ability of the invasive species as it expands its range (Burton et al., 2010). However, predicting the impacts of non-native species on novel ecosystems can be challenging (Griffen et al., 2021), particularly when a newly introduced non-native species coexists with components of the novel community elsewhere in its range (McDevitt et al., 2014).

The recent introduction of the greater white-toothed shrew *Crocidura russula* into the island of Ireland provides an example of how unpredictable the impacts of species invasions can be on the local fauna. *Crocidura russula* was likely accidentally introduced into Ireland in the early 2000s via horticultural imports from

mainland France (Gargan et al., 2016; McDevitt et al., 2014; O'Meara et al., 2014; Tosh et al., 2008). Prior to its arrival, the pygmy shrew *Sorex minutus* was the only species of shrew present in Ireland. *Sorex minutus* is sympatric with multiple shrew species across the European mainland, including *C. russula*. Differential resource use and niche separation among these insectivorous small mammals is known to be integral for facilitating multi-shrew communities (Rey et al., 2019) and this has been proposed to facilitate the sympatric existence of *S. minutus* (albeit in low abundance) with larger species of shrews in mainland Europe (Churchfield & Rychlik, 2006). Indeed, *S. minutus* and *C. russula* are the only shrew species present on the small island of Belle Île off northwestern France. Here, they are both abundant and coexist among a small mammal community similar to that in Ireland (Gargan et al., 2016; McDevitt et al., 2014). In contrast to Belle Île, the invasion and rapid spread of *C. russula* in Ireland is clearly associated with the local disappearance of *S. minutus* (McDevitt et al., 2014; Montgomery et al., 2012, 2015). Although *C. russula* is known to harbour a novel strain of pathogenic *Leptospira* and the potential role of novel pathogens/disease in this invasion-replacement event cannot be completely discounted, no evidence of disease onset was apparent after experimental infections (Nally et al., 2016). *Crocidura russula* is known to outcompete other shrew species when it colonises an area/island in other regions (Biedma et al., 2019; Cornette et al., 2015) but the exact mechanism(s) of how this occurs is uncertain. McDevitt et al. (2014) proposed that *S. minutus* may have experienced a competitive release on the island in the absence of other shrew species and is now not able to adapt quickly enough to a new invasive competitor.

This recent and ongoing invasion therefore presents us with a unique opportunity to examine resource competition between a native species and an invasive competitor before, during, and after an invasion in a real-time setting. There is a narrow region at the edge of the *C. russula* invasive range in Ireland where both shrew species overlap temporarily until *S. minutus* disappears in as little as a year (Figure 1; McDevitt et al., 2014). Further inside the well-established invasive range of *C. russula*, there is no evidence that *S. minutus* is still present (Montgomery et al., 2012, 2015; McDevitt et al., 2014; this study). The goal of this study was to investigate the diet and

FIGURE 1 Sampling sites in each of three transects (W: West; E: East; S: South) covering the different invasion stages (at the time of sampling) of *Crocidura russula* in Ireland ('before', 'during' and 'after') and the 'control' site in Belle Île. The presence of *C. russula* is indicated in green and *Sorex minutus* in orange.



body size (determined by length and weight) of both shrew species at different stages of the invasion (Figure 1). In addition, the diet and size of both species was investigated in Belle Île, where both species co-exist. Belle Île is an ideal natural 'control' site as the habitat types are similar to Ireland and it has the same small mammal community present (*C. russula*, *S. minutus*, *Clethrionomys glareolus* (bank vole) and *Apodemus sylvaticus* (wood mouse); McDevitt et al., 2014). To determine if resource competition is a contributing factor in the local replacement of *S. minutus* in response to the *C. russula* invasion in Ireland, DNA metabarcoding (Deagle et al., 2019; Pompanon et al., 2012) was applied to the gut contents of shrews to characterise their diet at different stages of the invasion in Ireland and Belle Île. Given that both species are generalist and opportunistic predators and their consumed prey is reflective of what is locally available in their environment (Bever, 1983; Brahmi et al., 2012; Churchfield & Rychlik, 2006; Churchfield & Sheftel, 1994; Pernetta, 1976), this allows us to investigate the levels of dietary overlap and interspecific competition between them (Arrizabalaga-Escudero et al., 2018; Nielsen et al., 2018; Razgour et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Study design

Sampling sites were chosen to investigate the impacts of the spread of *C. russula* in Ireland. These sites were chosen by first trapping where both species were present together in the 2012/2013 survey (McDevitt et al., 2014), establishing that *S. minutus* was now no longer present (i.e. has been replaced by *C. russula*) and then working

outwards to establish the new extent of *C. russula*'s range in 2017 (i.e. where both species were present together in 2017; Figure 1). The south of Ireland was then divided into three 'stages' of the invasion: 'before', 'during' and 'after' from the perspective of the impacted native *S. minutus* (Figure 1). 'Before' the invasion denotes where *C. russula* has not yet invaded and with only *S. minutus* present. 'During' the invasion is at the edge of the invasive range where *C. russula* first comes into contact with *S. minutus* and therefore both species overlap. 'After' the invasion is where only *C. russula* is present and *S. minutus* is no longer observed. Despite the homogeneous nature of the Irish landscape within the studied area (largely agricultural; McDevitt et al., 2014), geographical variation of available prey was accounted for by sampling shrews along eastern, western and southern transects through the invasive range (Figure 1). Due to the small size of the 'control' site in Belle Île (84 km²) where both species overlap, shrews were sampled from across the entire island.

To account for seasonal variation in diet (Grainger & Fairley, 1978), sampling was conducted over two seasonal time periods. The first seasonal sampling period took place from 19 August 2017 to 17 October 2017, referred to hereafter as 'summer/autumn'. The second sampling period took place from 16 February 2018 to 06 April 2018, referred to hereafter as 'winter/spring'. These dates by-pass the peak breeding months and should target the same cohort of shrews across the year.

2.2 | Sample collection

Trap sites were chosen at accessible hedgerows along secondary and tertiary roads adjacent to agricultural land (pasture or arable).

Shrews were trapped using trip-traps (Proctor Bros. Ltd., UK) with no bait (to avoid interference with dietary analyses). See Supporting Information and Figure S1 for more detail on trapping and sites. Shrews were immediately euthanised by cervical dislocation following guidelines set out by Sikes (2016). All trapping and procedures were performed under the appropriate licences: C21/2017 (National Parks and Wildlife Service, Ireland), AE18982/I323 (Health Products Regulatory Authority; Ireland) and A-75-1977 (Belle Île, France), and ethical approvals ST1617-55 (University of Salford, UK) and AREC-17-14 (University College Dublin, Ireland). Male and female adults were sampled. Each shrew was weighed using a 50g Pesola spring scale and body length (from nose to the tip of the tail) was measured using callipers for each sample. The gut tract (stomach and intestines) was removed and stored in absolute ethanol at a 1:4 (sample:ethanol) ratio (Egeter et al., 2015). To avoid cross-contamination, all dissections were performed on disposable bench covers and all tools were cleaned and flamed between samples. Gut contents were stored in ethanol at -20°C upon returning from the field to the lab (max. 12 days). A total of 99 *S. minutus* and 124 *C. russula* were caught from Ireland and a total of 40 *C. russula* and 40 *S. minutus* were caught from Belle Île (see Table S1 for sample sizes by transect and stage).

2.3 | Lab protocols

DNA was extracted from the gut contents using the Qiagen PowerSoil Kit (Qiagen Ltd.), with five extraction blanks. A 133bp fragment of the mtDNA COI gene was amplified from DNA extracts using the primers LepF1 (5'-ATTCHACDAAYCAYAARGAYATYGG-3') and EPT-long-univR (5'-ACTATAAAARAAAATYTDAYAAADGC RTG-3'; Gillet et al., 2015) according to the protocol described in Browett et al. (2021). These primers were previously shown to amplify the expected range of prey taxa in shrews in a multi-primer comparison study (Browett et al., 2021). The final library with a total of 303 samples, five extraction blanks and 20 PCR blanks was sequenced on two Illumina MiSeq runs using V2 2×150 bp cycle kits, both loaded at 9pM with a 5% PhiX (v3, Illumina) spike. See the Supporting Information for more detailed DNA extractions, PCR, library preparation and sequencing information.

2.4 | Bioinformatics and data filtering

Processing of raw sequence reads was performed using the Obitools metabarcoding software pipeline (Boyer et al., 2016). After aligning the paired-end reads, sequences with an alignment quality score >40 and a length between 128 and 138bp were retained (Browett et al., 2021). See the Supporting Information for further details of the bioinformatics undertaken. All MOTUs belonging to non-prey taxa (e.g. vertebrates and parasites) were removed. Samples with less than 1000 prey reads were removed. To mitigate false positive detections, MOTUs were removed from each sample if they were

represented by less than 0.1% of the total prey reads in that individual sample (Alberdi et al., 2018; Deagle et al., 2019).

To determine the coverage of samples, rarefaction curves and species accumulation curves were generated using the R package VEGAN (Oksanen et al., 2019). In addition, the *depth_cov()* function in the HILLDIV R package (Alberdi & Gilbert, 2019) was used to clarify if sufficient read depth was obtained for each sample, using the *qvalue* = 1 (equivalent to Shannon diversity measure). A second dataset containing a 'core' diet was created by removing rare prey taxa found in a single sample. This strategy is recommended for dietary studies, particularly for calculating resource overlap values (Arrizabalaga-Escudero et al., 2018; Brown et al., 2014).

2.5 | Diet composition and niche overlap and width

Three methods for quantifying the importance of different taxa to a population's diet were compared as described and recommended by Deagle et al. (2019). These were relative read abundance (RRA), percentage of occurrence (POO) and weighted percentage of occurrence (wPOO). All three metrics performed very similarly for quantifying the diet of groups of shrew samples, with discrepancies between certain prey orders (see Supporting Information for more details). The amplification biases seen between certain primers and prey taxonomic groups (Bista et al., 2018; Krehenwinkel et al., 2017) means that using the wPOO or POO metrics are the more conservative approach. There was little difference between these two metrics, and therefore only the POO values are reported in the main text while the RRA metrics are available in the Supporting Information for individuals.

To determine the compositional difference in prey taxa identified between different invasion stages in Ireland and Belle Île, PERMANOVA's were performed using the *adonis()* function in the VEGAN package in R (Oksanen et al., 2019). The multivariate distances of samples to the group centroid were calculated using *betadisper()* function in the VEGAN package and a permutation test for homogeneity of multivariate dispersions was used to determine if there was a similar level of variance between each group. These distances were calculated using reads transformed into RRAs and using the Bray-Curtis distance metric (using RRA), and the Jaccard distance metric (using presence-absence). These were performed for prey taxa grouped at MOTU, species, genus, family and order levels. NMDS plots were generated to visualise beta diversity measures, with enough dimensions to reduce stress to approximately 0.1. To determine if the close spatial proximity of certain sampling locations significantly influenced the observed differences in species' dietary compositions in Ireland, a Mantel test between the Bray-Curtis distance and geographic distance between sites for each species and overall was performed using the *mantel()* function in the VEGAN package with 10,000 permutations (Li et al., 2019).

The Pianka's (1973) niche overlap index (*O_{jk}*) was calculated in the R package ECOSIMR (Gotelli & Ellison, 2013) to identify overlap in diet between *S. minutus* and *C. russula* in different study sites.

To determine if resource overlap was significantly higher or lower than expected, a null model was created by running 10,000 resource utilisation simulations using randomisation function RA3, which reshuffles values within each predator group. Observed overlap values were compared with this null model to determine if the observed overlap is more or less than a random situation. The samples were grouped according to shrew species, Ireland versus Belle Île, and invasion stage. The niche width of each group was measured using the standardised Levin's index and Shannon diversity measure (for details on measurements see Razgour et al., 2011) on the POO values for each group using the R package SPAA (Zhang, 2016). If there was a large difference in sample size between groups, larger sample sizes were randomly subsampled to the same as the smallest group 50 times, and the average diversity scores were recorded.

3 | RESULTS

3.1 | Body measurements

The Belle Île population of *S. minutus* had larger individuals (mean \pm SE weight: 4.36 ± 0.12 g; length: 96.47 ± 0.84 mm) compared with individuals of the same species sampled in Ireland (weight: 3.34 ± 0.05 g; length 91.42 ± 0.45 mm; ANOVA post hoc Tukey $p < 0.0001$ for both weight and length; Table S2; Figure 2b and Figure S2). There is no evidence of a size difference between Irish *S. minutus* sampled 'before' the invasion (weight: 3.28 ± 0.06 g; length 90.62 ± 0.61 mm) and 'during' it (weight: 3.40 ± 0.07 g; length: 92.28 ± 0.66 mm). Conversely, *C. russula* in Ireland are larger compared with those in Belle Île. The *C. russula* sampled 'during' the invasion in Ireland were the largest sampled (weight: 11.45 ± 0.25 g; length: 117.73 ± 0.56 mm) compared with shrews sampled 'after' the invasion (weight: 10.58 ± 0.17 g; length: 114.73 ± 0.44 mm; $p < 0.0001$) and compared with Belle Île *C. russula* (weight: 9.84 ± 0.2 g; length: 111.81 ± 0.78 mm; $p < 0.002$; Table S2; Figure 2b and Figure S2). These overall patterns in weight and length were generally evident within a sampling season but also were more pronounced in samples collected in the spring period (Table S2; Figure S3).

3.2 | Sequencing

The two sequencing runs generated a total of 30,172,418 reads. After quality filtering of sequences and chimera removal, there were 21,091,503 reads across the 303 samples (average read depth of 68,459 reads per sample) and 25 negative controls. A full breakdown of retained sequences is provided in Table S3. The dataset using the sequence clustering threshold at 98% similarity yielded 33,801 non-singleton MOTUs. There were a total of 38,535 reads (0.18% of total reads) from 394 MOTUs identified in the negative controls. The collective read count of MOTUs in

the negative controls ranged from 1 to 14,606. The most prominent reads in the negative controls were from the family Soricidae (shrews) (Figure S4), most likely due to a combination of strong host amplification and 'tag jumping' (Schnell et al., 2015). Host amplification ranged between ~15.6% and ~99.95% in *C. russula* and between 0.14% and ~99% in *S. minutus*. These variable rates of host amplification are common among dietary studies of predators using DNA metabarcoding (Cuff et al., 2022).

The final dataset of prey items contained 994 MOTUs across 178 samples (59 *C. russula* and 119 *S. minutus*) with an average read depth of 34,955 prey reads per individual. Multiple samples of both species had notably less food remains inside the GI tract during dissection, which subsequently only returned host reads and the samples were filtered out. Previous work on *C. russula* showed that using alternative primer sets that do not amplify vertebrate DNA will still result in sample dropouts due to empty GI tracts (Browett et al., 2021). The sequencing depth showed sufficient coverage for each of the 178 samples, with richness ($q = 0$) showing 100% coverage and evenness ($q = 1$) values $>98\%$. Species accumulation curves show that at the species/MOTU level, the plateau was not reached for either species in either Ireland or Belle Île (see Figure S5). Sample coverage improves when aggregating taxa to higher levels, with a plateau reached at the order level. This is a common feature of dietary metabarcoding studies in insectivorous species (Tournayre et al., 2020).

3.3 | Diet composition

A wide range of invertebrate taxa are consumed by both species (Figures S6 and S7). When using RRA at the level of the taxonomic order of the prey for each individual shrew (Figure S8), it is evident that there is wide variation between individuals. This observed variation is consistent with the high level of variation between samples seen in the beta diversity results. RRA, POO and wPOO performed very similarly for quantifying the diet of groups of shrew samples (Figure S9). POO reveals a similar diet composition between Irish and Belle Île *S. minutus*. The Irish *S. minutus* population has a higher proportion of Diptera, Enterobryomorpha and Isopoda, while Belle Île *S. minutus* shows a higher rate of predation on Araneae (Figure 2a). Visually the composition of the *C. russula* diet differs for prey orders between Belle Île and the two invasion stages within Ireland, complementing the PERMANOVA results (Table 1). The composition of *C. russula* 'after' the invasion has the closest resemblance to the *S. minutus* diet in Ireland.

Many prey orders appear to remain consistent throughout the year, such as slugs and snails (Stylommatophora) and earthworms (Haplotaxida) in *C. russula* in Ireland (Figure S10). *Sorex minutus* shows the most notable seasonal shifts in prey orders (also shown by the PERMANOVA results; Table 1 and Table S4). *S. minutus* in Belle Île shows a decrease in consumption of Hemiptera in the spring with a dramatic increase in consumption of Araneae and Lepidoptera during the summer sampling period (Figure S10).

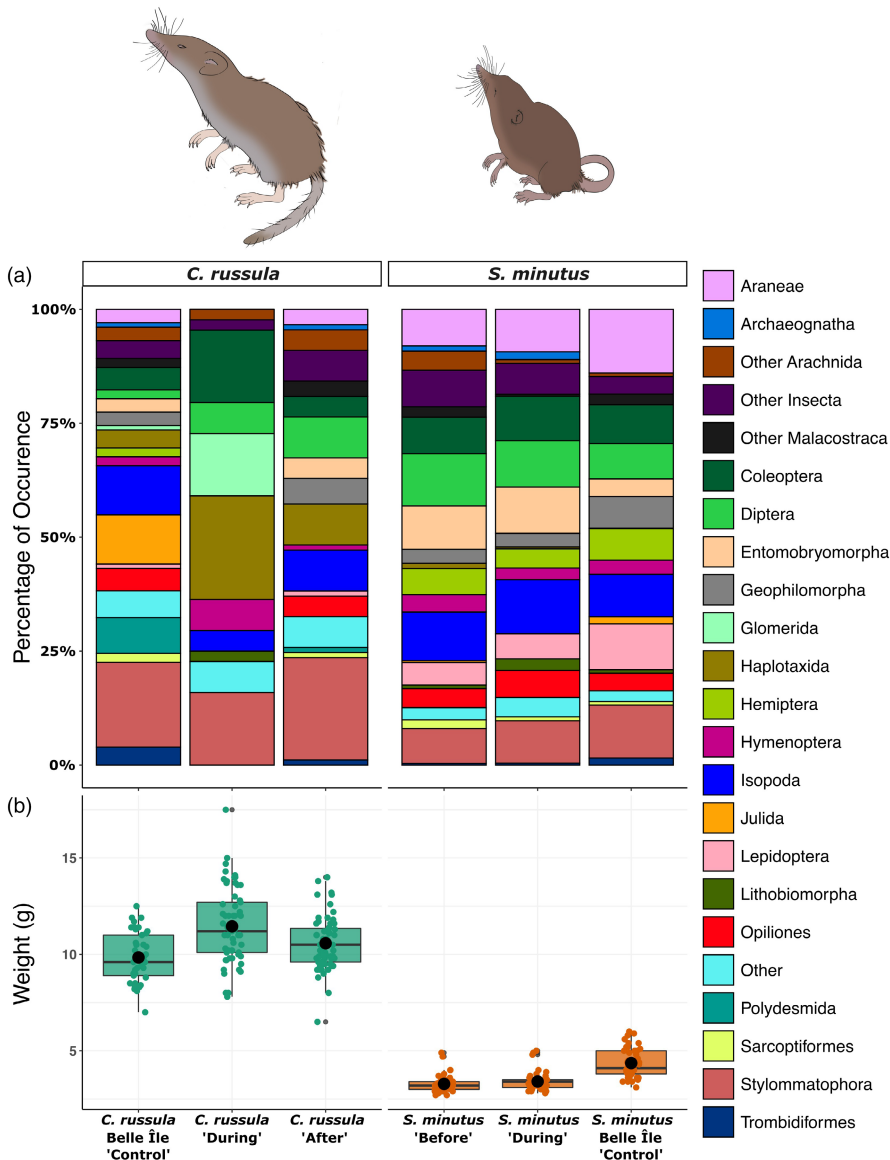


FIGURE 2 The composition of *Crocidura russula* and *Sorex minutus* diet (using percentage of occurrence) grouped to the level of invertebrate order (each represented by a unique colour) and for each invasion stage in Ireland ('before', 'during' and 'after') and the 'control' site in Belle Île (a). The weights of *C. russula* (green) and *S. minutus* (orange) for each invasion stage in Ireland and Belle Île (b).

3.4 | Niche width and overlap

The standardised Levin's index indicates that the niche width of both *S. minutus* and *C. russula* are similar (Table S5). The standardised Levin's index indicates that the niche width of Irish *C. russula* is wider than Belle Île *C. russula* at the MOTU (0.59 and 0.48), species (0.55 and 0.44) and genus (0.47 and 0.42, respectively) level but with similar niche width at the family level (0.44 and 0.43). However, the niche width at the order level is narrower for Irish *C. russula* compared with Belle Île (0.53 and 0.60, respectively). The Irish *S. minutus* population show a narrower niche width compared with Belle Île at the MOTU (0.50 and 0.58), species (0.45 and 0.54), genus (0.43 and 0.55) and family (0.48 and 0.59) level but a similar niche width at the order level (0.60 and 0.58, respectively; Table S5)

The PERMANOVA shows there is a difference in the composition of the diet at the MOTU level between shrew species ($R^2 = 0.02$, $p = 0.001$) and between Ireland and Belle Île ($R^2 = 0.02$, $p = 0.001$). Among the top 20 MOTUs contributing most to the differences

between shrews and between Ireland and Belle Île, there are mostly MOTUs belonging to Gastropoda (slugs and snails), Clitellata (worms) and Diplopoda (millipedes). There are notable differences in proportions of these orders in the diet of both shrews (Figure 2a). While PERMANOVAs showed no difference between Irish *C. russula* according to the season, transect or trap site, there was a small difference according to the invasion stage ($R^2 = 0.05$, $p = 0.029$). This difference is primarily caused by MOTUs from Insecta and Gastropoda. Season also showed no effect in Belle Île *C. russula*, but there was an observed difference between trap sites within the island ($R^2 = 0.45$, $p = 0.001$).

Irish *S. minutus* show a change in dietary composition according to season ($R^2 = 0.02$, $p = 0.001$), transect ($R^2 = 0.04$, $p = 0.001$) and trap site ($R^2 = 0.23$, $p = 0.001$). The majority of MOTUs contributing to the differences in transect and sampling sites are the same, primarily belonging to Coleoptera and Lepidoptera. The difference occurring between seasons is primarily driven by MOTUs ascribed to the Insecta class. Belle Île *S. minutus* also show slight differences in

TABLE 1 PERMANOVA results at the order level of identified prey taxa to show the prey composition dissimilarities using the Bray–Curtis distance method. Shrews are grouped according to species and island of capture. A PERMANOVA is performed on each group, examining multiple variables (season, trap site, invasion stage and transect) that contribute to compositional variance within each group. Variables are treated sequentially from top to bottom in each group. Significant values are indicated in bold (<0.05)

| Country | Species | Variable | df | F model | R ² | Pr(>F) |
|-----------|-------------------|-----------|----|---------|----------------|---------------|
| All | All | Country | 1 | 3.4747 | 0.01801 | 0.004 |
| | | Shrew | 1 | 13.7341 | 0.07119 | 0.001 |
| Belle Ile | <i>C. russula</i> | Season | 1 | 1.1322 | 0.04823 | 0.3112 |
| | | Trap Site | 8 | 1.168 | 0.39802 | 0.2607 |
| | <i>S. minutus</i> | Season | 1 | 2.4908 | 0.08217 | 0.0178 |
| | | Trap Site | 8 | 1.2276 | 0.32399 | 0.1515 |
| Ireland | <i>C. russula</i> | Season | 1 | 0.7589 | 0.01849 | 0.5877 |
| | | Stage | 1 | 6.1815 | 0.15061 | 0.0005 |
| | | Transect | 2 | 0.8314 | 0.04051 | 0.5855 |
| | | Trap Site | 11 | 1.131 | 0.30311 | 0.2642 |
| | <i>S. minutus</i> | Season | 1 | 2.4724 | 0.02589 | 0.0117 |
| | | Stage | 1 | 0.6685 | 0.007 | 0.7424 |
| | | Transect | 2 | 1.8652 | 0.03907 | 0.0217 |
| | | Trap Site | 19 | 1.1376 | 0.22636 | 0.1105 |

the composition of their diet between seasons ($R^2 = 0.08$, $p = 0.001$), but not trap sites. This shift in seasonal diet is primarily influenced by Insecta and Arachnida, which is noticeable in compositional change using POO measures (see Figure S10).

The NMDS plot shows that while all four stages between two species may be different in their centroid/core diet, there is still considerable overlap between samples (Figure 3). These patterns complement the PERMANOVA results, showing differences between groups but with low R^2 values that indicate that the tested variables explain less than 10% of the variation, except trap sites explaining up to 32% of the variation in *S. minutus* and 40% in *C. russula*. When considering only the Irish samples at different invasion stages, there is still considerable overlap. However, as MOTUs are agglomerated in genus, family and order, the *C. russula* sampled 'during' the invasion appear the most different, confirming the PERMANOVA results demonstrating that invasion stage explains a significant proportion of the variation in the diet of Irish *C. russula*. These plots suggest a higher similarity in diet between *C. russula* captured 'after' the invasion and *S. minutus* 'before' the invasion, particularly when prey species are grouped to higher taxonomic levels (Figure 3). There were no significant relationships between the spatial proximity of sites (Table S6) and similarities in dietary compositions (Mantel r for Irish *S. minutus*: 0.125, $p = 0.331$; Irish *C. russula*: 0.061, $p = 0.386$; Overall: -0.251 , $p = 0.960$).

The overlap of prey resources (measured using the Pianka's index; Ojk) between *C. russula* and *S. minutus* is generally high at ~37% to ~50% overlap, depending on whether all MOTUs or core MOTUs are used (Table 2). These are significantly higher values than would be expected at random. *Crocidura russula* and *S. minutus* show a higher dietary overlap in Belle Île (All MOTUs Ojk = 0.4617, $p < 0.05$; Core MOTUs Ojk = 0.50289) than Ireland (All MOTUs Ojk = 0.35772, $p < 0.01$; Core MOTUs Ojk = 0.37765). When splitting the samples in Ireland according to invasion stage, *S. minutus* have a much higher resource overlap with *C. russula* 'after' the invasion (~39%–46%) compared with with *C. russula* 'during' the invasion

(~11%–14%; Table 2). When accounting for all MOTUs, the level of overlap between *C. russula* 'after' the invasion and *S. minutus* is significantly higher than expected compared with simulated data (*S. minutus* 'during' Ojk = 0.40765, $p = 0.0167$; *S. minutus* 'before' Ojk = 0.38693, $p = 0.028$). This observation is consistent with the patterns shown in Figure 3.

4 | DISCUSSION

The impact of the rapidly expanding invasive range of *C. russula* in Ireland demonstrates the need to consider both the spatial and temporal context of species invasions in a real-time setting. This study shows that an invasive species can quickly alter its behaviour and adapt to a new environment, leading to negative impacts that were not previously predicted based on the co-existence of *C. russula* and *S. minutus* in other parts of their ranges. Here is an invasive species consuming larger prey taxa when it first enters an area before shifting its diet towards the smaller prey taxa that are more essential for the survival of the native species after it is established. This interspecific competition could then be playing a key role in the subsequent and rapid disappearance of the native species in response to the invader.

In Ireland, larger invertebrates such as worms (Haplotaxida), beetles (Coleoptera) and tough shelled millipedes (Glomerida) comprise a large portion of *C. russula*'s diet at the invasion wavefront ('during'), but this is then greatly reduced in the established 'after' invasion stage (Figure 2a). The combination of high abundance, small territories and broad diet means that *C. russula* can exhaust local resources (Genoud, 1985). As a result, the level of interspecific dietary overlap increases from between 11–14% 'during' the invasion to between 39% and 46% 'after' the invasion (Table 2), and the NMDS plot shows a higher overlap between *S. minutus* generally and *C. russula* once the invader has become established (Figure 3).

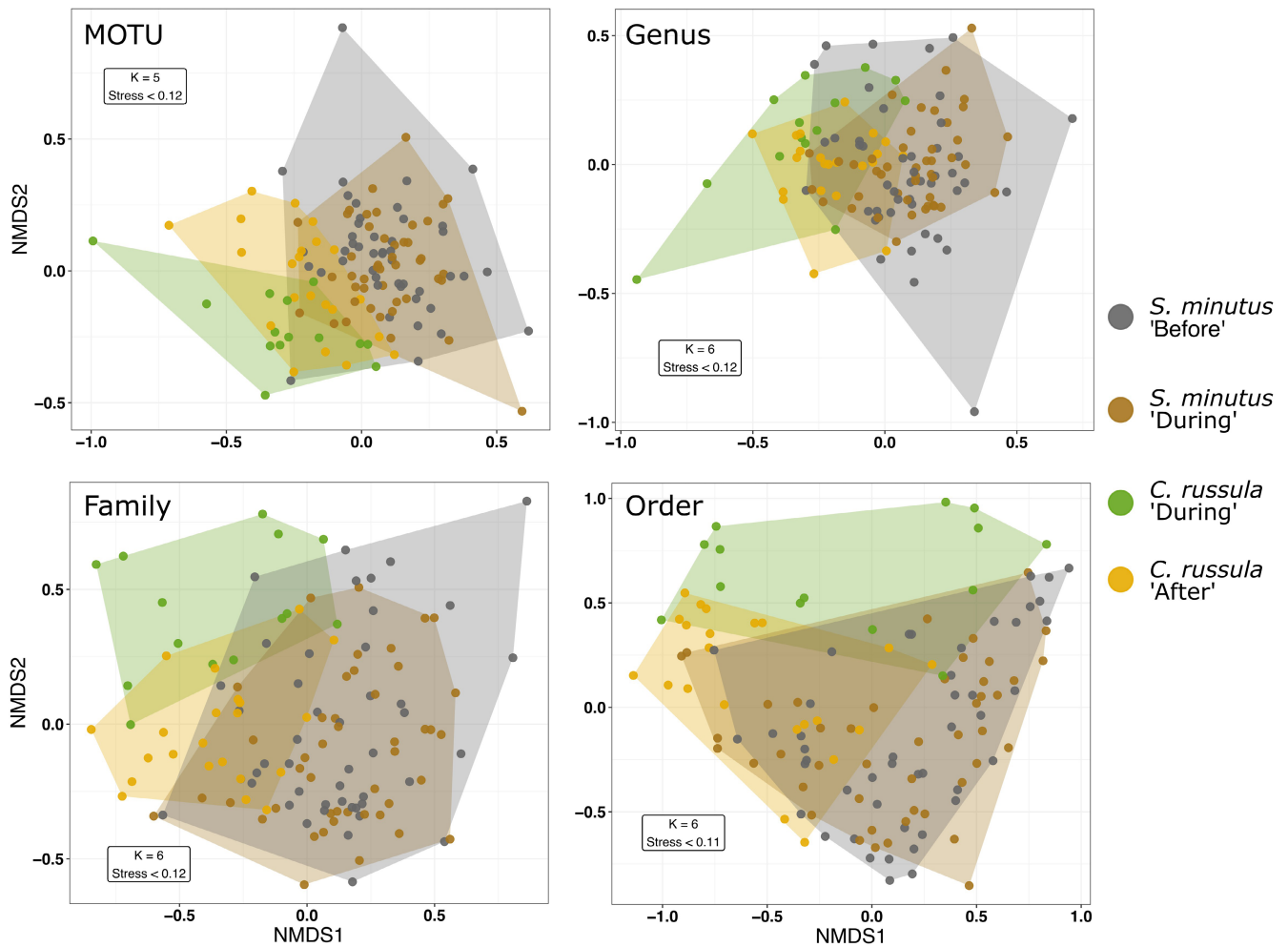


FIGURE 3 NMDS plot generated to visualise dietary overlap using the Bray–Curtis dissimilarity method using prey at the (clockwise from top left) molecular operational taxonomic unit (MOTU), genus, order and family level according to the invasion stages ('before', 'during' and 'after'; see main text) in Ireland for each species. Note there is less overlap between *C. russula* during the invasion (green) and the rest of the groups (corresponding to the dietary overlap results; Table 2).

| Interspecific and island comparisons | | | All MOTUs | Core MOTUs |
|--------------------------------------|-----|------------------------------|-----------|------------|
| <i>C. russula</i> –Belle Île | vs. | <i>C. russula</i> –Ireland | 0.42877* | 0.45655 |
| <i>C. russula</i> –Belle Île | vs. | <i>S. minutus</i> –Belle Île | 0.4617* | 0.50289 |
| <i>C. russula</i> –Ireland | vs. | <i>S. minutus</i> –Ireland | 0.35772** | 0.37765 |
| <i>S. minutus</i> –Belle Île | vs. | <i>S. minutus</i> –Ireland | 0.39034** | 0.47217* |
| <i>C. russula</i> –'During' | vs. | <i>S. minutus</i> –'During' | 0.11326 | 0.12801 |
| <i>C. russula</i> –'During' | vs. | <i>S. minutus</i> –'Before' | 0.13091 | 0.13604 |
| <i>C. russula</i> –'After' | vs. | <i>S. minutus</i> –'During' | 0.40765* | 0.45835* |
| <i>C. russula</i> –'After' | vs. | <i>S. minutus</i> –'Before' | 0.38693* | 0.4209 |

TABLE 2 Dietary overlap (Pianka index) values using percentage of occurrence (POO) and including all molecular operational taxonomic units (all MOTUs) and Core MOTUs (removing rare prey taxa found in a single sample). This includes comparisons between islands (Ireland and Belle Île) and the 'before', 'during' and 'after' stages of *Crocodyrus russula*'s invasion of Ireland (see main text). Index values range from 0 (no overlap) to 1 (complete overlap). Significance indicated at *0.05; **0.01

The invasion appears to be occurring in 'layers'. Individuals from the first invading layer of *C. russula* ('during') are 20% larger in body mass (Figure 2b) and longer (Figures S2 and S3) than those 'after' the invasion. This may be the result of decreased intraspecific competition and/or investment in traits associated with increased dispersal abilities (Burton et al., 2010; Phillips et al., 2006). Their larger size

may aid in their ability to predate on invertebrates that are too large for *S. minutus*, thus initially reducing competitive pressure. Previous studies have shown that shrews that differ greatly in size tend to have reduced niche overlap compared with shrew species closer in size (Churchfield & Rychlik, 2006). This would explain why both *C. russula* and *S. minutus* temporarily coexist at a restricted area where

their ranges first meet (McDevitt et al., 2014). The relatively narrow niche width of *C. russula* (Table S5) provides some contradiction to previous claims that predation in shrews is likely opportunistic with little selection of prey (Castien & Gosalbez, 1999). The second established layer of *C. russula* ('after') appear to be altering their diet to smaller prey taxa (Figure 2b). The accompanying decrease in body mass in the second layer could suggest reduced energy intake from reduced food resources after the first layer (Seymour et al., 2005). This second layer of *C. russula* is what likely out-competes *S. minutus* for small prey resources that are key for their survival (Churchfield & Rychlik, 2006; Pernetta, 1976). This is why there is only a brief area of overlap, which eventually means they cannot coexist and *S. minutus* rapidly declines/disappears in as little as 1 year (McDevitt et al., 2014).

The dietary mechanisms by which this displacement occurs are subtle and reveal the importance of the DNA metabarcoding approach used here and its ability to identify prey tax beyond the order/family level (as is typical with morphology-based analysis of diet; Browett et al., 2020; Tournayre et al., 2020). The Pianka index identified considerable overlap in diet between these two shrews in both Ireland (up to 38%) and Belle Île (up to 50%; Table 2). This is supported by the NMDS plots (Figure 3) and PERMANOVA showing minimal differences in the composition of prey between shrew species and country (Table 1). This level of dietary overlap has been seen between sympatric populations of water shrews *Neomys fodiens* and *S. minutus* in Poland (44% overlap), which was considered low for shrews (Churchfield & Rychlik, 2006). Overlap between the diet of sympatric shrews is considered high in general, and multi-species communities' likely function as a result of subtle differences between habitat and resource use (Churchfield & Sheftel, 1994). Therefore, the level of dietary overlap alone may be enough to explain their coexistence in Belle Île, but not Ireland. The POO values indicate that the majority of prey orders in Ireland are consumed by both predators (Figure 2a). In contrast, there are key taxa that are consumed in Belle Île by one predator but not the other. There is an increased consumption of the orders Araneae, Hemiptera and Lepidoptera by Belle Île compared with Irish *S. minutus*, but not consumed by Belle Île *C. russula* (Figure 2 and Figure S8). Instead, Belle Île *C. russula* have approx. 25% of their diet consisting of worms (Haplotaxida) and millipedes (Glomerida, Julida and Polydesmida), of which Belle Île *S. minutus* does not predate on. These prey orders may be key to providing competitive release between the shrews in Belle Île. Belle Île *S. minutus* also have a drastically increased consumption of Lepidoptera during the winter (Figure S10), similar to previous observations of winter spikes of consuming Lepidopteran larvae using morphological approaches (Butterfield et al., 1981; Pernetta, 1976). While DNA metabarcoding cannot identify life stage, it has identified a large proportion of this winter spike to be *Xestia xanthographa*. This moth species over-winters as nocturnal larvae (up to 35 mm in size), feeding on various grasses (Skinner & Wilson, 2009). The nocturnal behaviour of *S. minutus* means they can take advantage of this slow moving and substantial food source during the less favourable winter conditions free from competition from *C. russula*. Another study

in the Netherlands has also shown that partial niche segregation between *S. minutus* and the larger common shrew *Sorex araneus* over seasons may reduce interspecific competition (Ellenbroek, 1980). The small difference in prey taxa consumed by *S. minutus* in Belle Île between seasons suggests that they are predated on more readily available taxa between seasons, such as the apparent switch from Hemiptera in the summer to Lepidoptera in the winter (Figure S10).

Another factor affecting resource use could be the morphology of the shrews themselves. Bite force and mechanical leverage of a shrew's mandibles can determine the limits of prey size they can capture and consume (Cornette et al., 2015). Vega et al. (2016) examined the variation of shape and size of mandibles and skulls from *S. minutus* samples from various European regions including Ireland, Belle Île and multiple other islands. This study showed that *S. minutus* can exhibit morphological variability between different regions and islands in response to various environmental factors such as food availability and the presence of competitors. It also showed that the mandible size and shape of Irish *S. minutus* are distinct from other populations, likely a reflection of their long-term isolation from other European populations (Vega et al., 2020). *Sorex minutus* from Belle Île are more similar to continental populations where they coexist with other species of shrews. The larger size of Belle Île individuals determined by this study (Figure 2b) and the mandible shape inferred from Vega et al. (2016) may allow them to avail of a wider range of sizes of prey, which could explain the wider niche breadth measured by the Standardised Levin's index (Table S5; Cornette et al., 2015). For example, species of Araneae consumed by Belle Île *S. minutus* are larger wolf spiders from the genera *Pardosa* and *Alopecosa* that can be up to 11 mm in size, providing a substantial energy resource. Irish *S. minutus* show a reliance on smaller spiders such as *Pachygnatha* spp. measuring between 3 and 6 mm (Nentwig et al., 2020).

5 | CONCLUSIONS

C. russula is known to outcompete and displace other shrews on islands (Cornette et al., 2015) and here we have shown just how rapidly this can occur in real-time (McDevitt et al., 2014). Given that the eradication of an invasive shrew like *C. russula* on an island of Ireland's size would not be logistically feasible (Seymour et al., 2005), this is obviously a concerning scenario for the island's fauna. This obviously goes beyond the invasive shrew's impacts on *S. minutus*. In terms of small mammal invasions on islands, there has been justifiably a lot of focus on the impacts caused by invasive commensals such as rats (*Rattus* spp.) and mice (*Mus* spp.) on other vertebrates (e.g. Jones et al., 2016), with perhaps less focus on their substantial impacts on invertebrates (St. Clair, 2011). In this study, we have shown that this invasive shrew initially preys on larger invertebrate taxa when they first invade an area before rapidly shifting towards smaller prey taxa after they become established. If they are potentially exhausting local resources of larger invertebrate species (Genoud, 1985), subsequent changes in terrestrial invertebrate communities can

of course have severe impacts further downstream on ecosystem functioning and services (Sanchez-Bayo & Wyckhuys, 2019). As powerful as DNA metabarcoding is becoming for characterising dietary interactions between species (Cuff et al., 2022; Nielsen et al., 2018), it is vital that further research is undertaken to describe and quantify the local invertebrate prey communities during this invasion-replacement event. Shrews have extremely high metabolic rates, which means the frequent and rapid location of prey is the most important factor for their short-term survival. Therefore, their consumed prey is reflective of what is available to them (Churchfield & Rychlik, 2006; Churchfield & Sheftel, 1994). However, it is still important that future studies carry out comparisons between what is being directly consumed versus what is available to the shrews at different sampling sites (while still taking into consideration the caveats of the semi-quantitative nature of DNA metabarcoding; Wray et al., 2021). In parallel, improving local reference databases, primer optimisation (Cuff et al., 2022) and using non-invasively collected faecal samples (which would also allow for individual-level identification through genotyping) for future DNA metabarcoding studies would also be warranted (Curran et al., 2022) to determine if *C. russula* is altering the composition of Ireland's invertebrate community as its invasion rapidly progresses and what potential impacts this may have on the wider ecosystem on the island.

AUTHOR CONTRIBUTIONS

Allan D. McDevitt, Samuel S. Browett, Denise B. O'Meara, Jon M. Yearsley and Jeremy B. Searle conceived, and Samuel S. Browett, Allan D. McDevitt, Jon M. Yearsley, Rachael E. Antwis, Kevin J. Bown, Deborah A. Dawson and Owen S. Wangenstein designed the study. Samuel S. Browett, Stephen S. Browett and Rebecca Synnott performed the shrew sampling. Samuel S. Browett and Rebecca Synnott performed the laboratory work. Samuel S. Browett analysed the data. Samuel S. Browett and Allan D. McDevitt wrote the paper, and all authors contributed to editing, discussions and approval of the final manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw sequencing data are available on Dryad at <https://doi.org/10.5061/dryad.rr4xgxdcq> (Browett et al., 2022a), and all bioinformatic steps and scripts can be found on Zenodo at <https://doi.org/10.5281/zenodo.7349030> (Browett et al., 2022b).

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SUPPORTING INFORMATION

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

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