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## Parasite community dynamics in an invasive vole – From focal introduction to wave front

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## ABSTRACT

Multiple parasite species simultaneously infecting a host can interact with one another, which has the potential to influence host–parasite interactions. Invasive species typically lose members of their parasite community during the invasion process. Not only do the founding population escape their parasites, but the rapid range expansion of invaders once in the invaded range can lead to additional stochastic loss of parasites. As such, parasite community dynamics may change along an invasion gradient, with consequences for host invasion success. Here, we use the bank vole, *Myodes glareolus*, introduced as a small founding population at a point source in the Republic of Ireland in c.1920's and its ecto- and endoparasites to ask: i) how does the parasite community vary across an invasion gradient, and ii) are parasite community associations driven by host traits and/or distance from the point of host introduction? We sampled the parasite community of *M. glareolus* at the proposed focal site of introduction, at mid-wave and the invasion front, and used a parasite interactivity index and statistical models to determine the potential for the parasite community to interact. Bank voles harboured up to six different parasite taxa, with a significantly higher parasite interactivity index at the foci of introduction ( $z = 2.33$ ,  $p = 0.02$ ) than elsewhere, suggesting the most established parasite community has greater opportunities to interact. All but one of four synergistic parasite community associations were driven by host traits; sex and body mass. The remaining parasite–parasite associations occurred at the mid-point of the invasion wave, suggesting that specific parasite–parasite interactions are not mediated by distance from a focal point of host introduction. We propose that host traits rather than location along an invasion gradient are more likely to determine parasite–parasite interactions in the invasive bank vole.

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### 1. Introduction

The release of a species from the constraints of their native biotic community can give rise to changes in traits, resulting in explosive demographics within the invasive range (Colautti et al., 2004). Invasive species can be more fecund, larger in size and reach greater population sizes than their native counterparts (Blaustein et al., 1983; Keane and Crawley, 2002; Parker et al., 2013). A widely supported mechanism underlying these changed traits, and thus the success of invasive species is the enemy release hypothesis, whereby loss, or reduction of natural enemies; both predators and parasites, is translated into increased host fitness (Keane and Crawley, 2002). The regulatory effects of enemies are

not equal, however. The heterogeneity of enemy release is most clearly demonstrated by parasites, as opposed to predators, where the effects upon hosts range from acute infections to almost benign (Leggett et al., 2017). Parasites can have strong regulatory effects on their host population size (Hudson et al., 1998), have positive effects on life history traits (Telfer et al., 2002), and can even be essential for maintaining biodiversity at an ecosystem level (Hudson et al., 2006).

During the invasion process there may be stochastic loss of parasite species that results in the invasive population harbouring only a subset of the parasite community of the comparable native population (Blaustein et al., 1983; Mitchell and Power, 2003; Torchin et al., 2003; Colautti et al., 2004; Phillips et al., 2010). Empirical meta-analyses have quantified that across multiple host species, the parasite diversity in the native range consists, on average, of 16 species, whilst invasive conspecifics harbour only three species of this original community (Torchin et al., 2003). As

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the founding population expands across an invasion gradient, the parasite community is subject to further potential parasite losses as a function of host dispersal. At the invasion front, the host population density as well as contact rates between individuals are often low, reducing the probability of parasite transmission (Morand and Poulin, 1998; Phillips et al., 2010). Additionally, stochastic fade-out of parasite species can occur due to low parasite abundance in the advancing invader, leading to some parasite species becoming locally extinct, and a 'lag effect', where some parasite species are absent from hosts at the invasion front (Bell and Burt, 1991; Phillips et al., 2010; Coates et al., 2017), giving them a competitive advantage.

Importantly, the parasite community within a host interacts; with antagonistic and/or synergistic interactions occurring between parasite species (Lello et al., 2004; Graham, 2008; Telfer et al., 2010). If, for example, synergistic interactions exist in the parasite community, such that the presence of one parasite species increases the abundance of another (e.g., Behnke et al., 2009; Lass et al., 2013), then, it follows that loss of one of these species in a community could lead to a reduced abundance of the other. Alternatively, if parasite-parasite interactions are antagonistic, i.e., one parasite suppresses another (e.g., Ferrari et al., 2009), loss of one of these may result in an increase of the other; a competitive release. Ultimately, the underlying mechanisms driving parasite interactions can include direct competition for resources, such as space, or indirect interactions, mediated for example by host immunity, the latter of which is linked to host traits, such as sex and body mass (Lello et al., 2013). The presence (or absence) of a given parasite species and/or the predominance of a given host trait in the host population may therefore promote a given parasite community. Whilst much work in invasion ecology has focused on the effect of parasite loss on the evolution of increased competitive ability of the host (see Strayer et al., 2006), because parasites interact with one another and the host, it is pertinent to ask how parasite loss may alter the parasite community of invasive species, and ultimately, invasion success. The first step in doing so is to determine if a parasite community interacts.

Determining whether parasites interact has been the focus of much research since Holmes's seminal papers in the 1960's (Holmes, 1961, 1962). The methods used to determine whether particular species interact include statistical methods (e.g., Lello et al., 2004; Telfer et al., 2010) and empirical perturbation (e.g., Ferrari et al., 2009). Interactions between parasites may be erroneously detected from observational data (Fenton et al., 2010), and can be inherently difficult to detect unless empirical perturbation is used, or in the absence of perturbation, a generalised linear mixed model (GLMM) approach on longitudinal data (Fenton et al., 2014). In natural systems, however, empirical perturbation is not always possible, and longitudinal data may be logistically difficult to collect. Insight into community structure may be gained by quantifying the degree of interaction. Broadly speaking, communities can be categorised into two extreme groups; interactive vs. isolationist (Holmes and Price, 1986). Parasite communities are generally believed to lie somewhere along the interactive-to-isolationist continuum, i.e., diverse assemblages of species with high infection rates in which interspecific interactions are likely, to low diversity communities where interactions are unlikely. Qualitative indices of interactive versus isolationist communities have been proposed (e.g. Poulin and Luque, 2003), which are calculated across hosts at a population level. Ferrari et al. (2016) have recently developed an index at an individual level, giving an indication of the degree of interaction within a community and allowing comparisons to occur across multiple individuals. If parasite interactions have an evolutionary history and interspecific interactions play an important structuring role they tend to be interactive, or if interactions are

unlikely, then the community is isolationist (Poulin and Luque, 2003). Across an invasion gradient, we expect parasite interactions to be greater in more established populations and weaker at the invasion front where loss of parasites, due to lag effects, may have altered community structure.

Here we ask, 'does the parasite community, and the associations between parasites differ in an invasive species along an invasion gradient?' and second, 'do host traits and/or invasion location drive parasite associations?' Using a quantitative index (see Ferrari et al., 2016) and a GLMM approach we quantified the parasite abundance, diversity and investigated the parasite community associations of the bank vole (*Myodes glareolus*), in its invaded range in the Republic of Ireland. The bank vole has a wide distribution across Europe, and has been absent from Ireland due to its isolation from Britain, which occurred during the rising sea levels at the end of the most recent glaciations (Williamson, 1996). The bank vole was, purportedly first introduced into Ireland in the 1920's on the south side of the river Shannon (Stuart et al., 2007); however the first official recording of a bank vole was in Listowel, County Kerry in 1964 (Claassens and O'Gorman, 1965). From this focal point of introduction the bank vole has spread across the Republic of Ireland at an estimated rate of 2–4 km per year (Montgomery et al., 2012; White et al., 2012). The invasive vole in the Republic of Ireland represents an excellent model system for studying enemy release with respect to parasites, because many of the predators from the native range of mainland Europe are also found in the invaded range.

## 2. Material and methods

### 2.1. Sampling along an invasion gradient

Live-trapping of bank voles (*Myodes glareolus*) was carried out in suitable habitat, typically road-side verges, at three transects across an invasion gradient in the Republic of Ireland between August and December 2010. Each transect originated from the focal point of introduction of *M. glareolus*, and radiated out from there to the invasion wave front with three samples taken for each transect, so representing a historical sample, or 'wave' of the invasion process (Fig. 1, results). Two sites were sampled at the purported focal introduction location in County Kerry; Adare (52° 33' 51.6780" N, 8° 47' 23.8380" W) and Curraghchase (52° 37' 1.2576" N, 8° 52' 39.1940" W), three sites were sampled at a mid-point location along the invasion wave; Gort (53° 4' 6.0600" N, 8° 49' 10.7828" W), Nenagh (52° 51' 57.8808" N, 8° 11' 47.7769" W) and Cashel (52° 31' 1.8156" N, 7° 53' 41.0507" W), and a further three sites at the invasion front; Tuam (53° 30' 55.1196" N, 8° 51' 14.9933" W), Birr (53° 5' 48.5304" N, 7° 54' 39.1838" W) and New Ross (52° 23' 45.7332" N, 6° 56' 43.5944" W).

At each site, up to 50 Ugglan multiple-capture traps (Grahnbab, Sweden) were set in three transects and were baited with wild bird seed and apple as a source of moisture, and contained straw for bedding. Traps were checked every 4 h and sampling continued until the first 20 bank voles of any sex had been caught at each site, except at one of the sites at the focal point of introduction, Curraghchase, where 40 animals were sampled, to ensure that each section of the invasion gradient had 60 animals sampled. Upon capture, animals were weighed and sexed, and were euthanised with a lethal dose of anaesthetic (Isoflurane, VetEquip Inc., UK) followed by cervical dislocation. All work was approved by the Ethical Committee at Cardiff University. Animals were transported to the laboratory for parasite identification.

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