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Reduced helminth parasitism in the introduced bank vole (*Myodes glareolus*): More parasites lost than gained

Karen C. Loxton [a, *], Colin Lawton [b], Peter Stafford [a], Celia V. Holland [a]

[a] Department of Zoology, School of Natural Sciences, Trinity College Dublin, Ireland
[b] School of Natural Sciences, National University of Ireland Galway, Ireland

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ABSTRACT

Introduced species are often less parasitised compared to their native counterparts and to ecologically similar hosts in the new environment. Reduced parasitism may come about due to both the loss of original parasites and low acquisition of novel parasites. In this study we investigated the intestinal helminth parasites of the introduced bank vole (*Myodes glareolus*) in Ireland. Results were compared to data from other European studies and to the intestinal helminth fauna of an ecologically similar native rodent in Ireland, the wood mouse (*Apodemus sylvaticus*). The helminth fauna of introduced bank voles exhibited low diversity with only 3 species recovered: *Aspiculuris tianjinensis*; *Aonchotheca murissylvatici* and *Taenia martis* larvae. In particular, no adult parasites with indirect life-cycles were found in bank voles suggesting that indirectly transmitted parasites are less likely to establish in invasive hosts. Also, the results of this study add support to the enemy release hypothesis.

1. Introduction

Studies across a range of plant and animal taxa have found that species introduced into a novel environment often escape many of their own parasites during the course of invasion and establishment (Torchin et al., 2003; Torchin and Mitchell, 2004). While invaders encounter and accumulate new parasites these do not always replace those that have been lost. Invasive species overall remain less parasitised than both conspecifics in their original range and ecologically similar native species in the new location (Torchin et al., 2002; Roche et al., 2010).

The number of parasite species that invaders acquire can depend in large part on the composition of the native host community. Parasites typically have greater infection success in closely related hosts as these share similar physiological and immunological characteristics (Kennedy and Bush, 1994; Perlman and Jaenike, 2003) and environments rich in host species are also those rich in parasite species (Hechinger and Lafferty, 2005; Thieltges et al., 2011). Thus, species-rich environments, particularly those with numerous host species closely related to or ecologically similar to the invading species are likely to provide increased opportunities for invaders to acquire novel parasites.

The bank vole was first recorded in Ireland near Listowel, Co. Kerry, in 1964 (Claassens and O'Gorman, 1965), though its introduction was likely much earlier. Stuart et al. (2007) using mitochondrial (mt) cytochrome b gene sequences found a close genetic relationship between bank voles introduced to Ireland and those native to Germany. From this information the authors suggest that a small population of bank voles was transported to Ireland along with earth moving equipment for the River Shannon hydroelectical scheme, which pushes date of introduction from previous estimations to the late 1920s. The bank vole now occupies approximately one-third of the south-west of Ireland and is continuing to expand its range at a rate of between 1.79 and 2.5 km-year (Montgomery et al., 2012; White and Perkins, 2012).

Ireland has a depauperate mammal community with only three species of small ground-dwelling rodents: the brown rat (*Rattus norvegicus*), wood mouse (*Apodemus sylvaticus*) and house mouse (*Mus musculus*) (Marnell et al., 2009; Montgomery et al., 2014). In particular, no vole (arvicoline) species are native to Ireland (Marnell et al., 2009). The bank vole is however unusual among the arvicoline rodents, showing ecological characteristics more similar to mice (muridae). Unlike other vole species, which are found in open habitats, bank voles are strongly associated with areas of heavy vegetation and show food preferences that are intermediate between insectivorous/granivorous murine and herbivorous

* Corresponding author.
E-mail address: loxtonk@tcd.ie (K.C. Loxton).

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arvicoline species (Kikkawa, 1964; Butet and Delettre, 2011). Bank voles, therefore, have ecological characteristics similar to the Irish native wood mouse, which is found alongside the bank vole throughout its invaded range in Ireland. The probability that two species will share parasites is not only a function of their phylogenetic relatedness, but also their ecological similarity (Poulin and Mouillot, 2004), and rodent species that share similar ecologies can also have similar parasite communities (Begon et al., 1999).

Here, we tested the hypothesis that invasion of a novel environment is followed by a reduction in helminth diversity and burden in the invasive host. We examined the intestinal helminth community of the introduced bank vole in Ireland and compared it to the helminth community of the ecologically similar wood mouse, as well as to published studies of helminth fauna of bank voles in its native range across Europe.

2. Materials and methods

Two sites were selected within the present range of the bank vole in Ireland. Coole Nature Reserve (53°07.809'N; −8°85.771'W) and Unclin Wood, Merlin Park (53°27.836'N; −8°99.835'W), both located in County Galway. The bank vole was first recorded in County Galway in 1985 (Fairley, 1985) and within the Galway City area in 2003 (McHugh and Lawton, 2005). Coole Nature Reserve is part of the Coole-Garryland complex special area of conservation. Vegetation is comprised of mixed deciduous forest, mainly oak (*Quercus robur*), ash (*Fraxinus excelsior*) and hazel (*Corylus avellana*) and a ground layer of ivy (*Hedera helix*). The woodland included patches of conifer stands where ground cover was scarce. Unclin Wood in Merlin Park is urban woodland situated on the eastern edge of Galway City. The woodland was similar to Coole Woods consisting of native oak-ash-hazel broadleaved woodland and conifers.

Trapping was carried out using standard Longworth traps baited with peanuts during the autumn of 2011 and 2012. Traps were placed in pairs 10 m apart along straight line transects and left in situ overnight. Sites were initially trapped for three consecutive nights and then revisited if needed until a minimum sample size of at least 15 animals per site was obtained, as recommended by Jovani and Tella (2006). Sampling protocols were chosen to minimise animal stress and suffering. Traps were collected early morning and animals were euthanised as soon as possible. We deeply anaesthetised animals with 96% Isoflorine prior to cervical dislocation to minimise handling of the animals and to reduce pain, suffering and distress in line with Directive 2010/63/EU. The entire intestinal tract from oesophagus to anus was removed and stored in 70% alcohol until examination. The surface of the liver and body cavity were checked and any adult or juvenile helminths were removed and stored. Helminths were identified from the published literature (Harvey and Channon, 1956; Tenora et al., 1983; Montgomery et al., 1987; Justine and de Roguin, 1990; Khalil et al., 1994; Loos-Frank, 2000). Molecular analyses of *Aspiculuris* sp. samples confirmed this species was *Aspiculuris tianjinensis*, as reported in Behnke et al. (2015).

Eye lenses were dissected out and stored in 10% formalin for at least 3 months. After this time lenses were removed from formalin, washed in deionised water and dried in a fan assisted oven at 60° for 48 h. The weight of both lenses were recorded the nearest 0.0001 g. Eye lens weight and the morphometric measures body weight and nose to anus length were fitted to a Principal Component Analyses. Principal component 1 was then used to order the mice and allocate them to three age classes: juvenile, adult and mature (Table 1). Visual assessments of maturity were used to help allocate mice at the limits at each category (Behnke et al., 2001).

Helminth community structure was statistically analysed at two hierarchical levels: the infracommunity and component community (Bush et al., 1997). Community structure was measured following methods described by Kennedy and Hartvigsen (2000) and Behnke et al. (2001). Measures of component community structure are:

- Total species richness
- The Berger-Parker Dominance Index. This index measures the proportion of the sample made up by the dominant species. The dominant species is the species showing the highest proportion in each data set. The index is calculated as $d = \frac{N_{max}}{N}$ where N_{max} is the number of individuals of the most abundant species and N is the total of all individuals in the sample.
- Simpson's Index of Diversity calculated as $D = 1 - \frac{\sum in(n-1)}{N(N-1)}$ where n is the total number of individuals of a particular species and $N =$ the total number of individuals of all species. Simpson's Index takes into account both the number of species present and the relative abundance of each species. As species richness and evenness increase, so diversity (D) increases.

Measures of infracommunity structure are:

- Mean species richness – the average number of parasite species per host (Montgomery and Montgomery, 1989).
- Maximum number of species per host.
- Infracommunity diversity was measured by the mean and maximum Brillouin's Index, appropriate for fully censured communities (Pielou, 1966). The index was calculated per host (infected and uninfected) as $HB = \frac{\ln(N!) - \sum \ln(ni!)}{N}$, where N is the total number of individuals in the sample, *ni* is the number of individuals of species *i*, ln(x) refers to the natural logarithm of x.
- Mean intensity was calculated as the mean number of helminths in infected animals only (Bush et al., 1997).
- Prevalence (%) is defined as the number of hosts infected with one or more helminth species divided by all hosts examined (Bush et al., 1997).

All statistical analyses were performed in the R statistical computing environment (R Development Core Team, 2014) version 3.0.2 with additional tools from statistical packages cited in text. Prevalence data was calculated with the Clopper-Pearson exact 95% confidence intervals (CL_{95}) using the function "exactci" in the R package PropCIs (Scherer, 2010).

Generalized linear models are recommended for the analyses of aggregated parasite data (Wilson and Grenfell, 1997; O'Hara and Kotze, 2010). Intensity was modelled with the modified negative binomial GLM from the MASS package (Venables and Ripley, 2002).

Table 1
Approximate ranges of morphometric measures used to assign wood mice and bank voles to three age classes.

	Juvenile		Adult		Mature	
	Wood mice	Bank vole	Wood mice	Bank vole	Wood mice	Bank vole
Eye lens (mg)	7–12	2–5	12–19	4–7	>19	>6
Weight (g)	8–14	8–17	14–22	14–23	>22	>20
Nose to anus length (mm)	18–77	66–85	77–95	75–100	>95	>85

Full factorial models incorporated all factors. Factors included measures of age (3 levels: Juvenile, Adult, Mature); site (2 levels: Coole, Merlin); year (2 levels: 2011 and 2012) and host species (2 levels: bank vole and wood mice). Models were simplified using the step procedure to derive the minimal sufficient model and the significance of remaining factors was determined by removing them from the model and testing for changes in deviance with chi-squared (χ^2) test for binomial and Poisson errors; likelihood ratio tests (LR) for negative binomial errors and F test for quasi-poisson errors. Residual deviance of the simplified model was used to perform a goodness of fit test for the overall model. Models were said to fit reasonably well when the goodness-of-fit χ^2 test was not statistically significant. Where models could not be fitted satisfactorily non-parametric tests were used to examine each of the main effects in turn. Mann-Whitney *U* test was used for 2 group comparisons and the Kruskal-Wallis test for comparison with more than 2 groups.

3. Results

A total of 329 rodents were collected: 152 wood mice and 177 bank voles. Nine species of helminth were recovered overall, 6 species from only wood mice, 1 species unique to bank voles and 2 species found in both voles and wood mice (Table 2 and Table 3).

Overall wood mice had a higher prevalence of helminth infection (GLM, family = binomial, host species: $\chi^2_1 = 33.1$, $P = 0.001$) (Tables 2 and 3). There was increase in the mean number of hosts infected in 2012. The increase was significant in bank voles (GLM, family = binomial, year: $\chi^2_1 = 19.7$, $P = 0.001$). In both hosts the effect of helminth prevalence on age class was significant. Helminth prevalence rose through the age classes and hosts classified as mature had the highest infection prevalence (GLM, family = binomial, age class: χ^2_2 bank vole = 17.7, $P = 0.001$; wood mouse = 18.3, $P = 0.001$) (Tables 2 and 3).

Where full factorial models for intensity could not be fitted satisfactorily each factor was tested singly using non-parametric statistics. Helminth intensity was greater in wood mice than in bank voles (Mann-Whitney *U* test, host species: $z = 3.6$, P = 0.001) (Tables 2 and 3). Infection intensity increased in both host species in 2012 (bank vole GLM, family = negative binomial, year: $LR_1 = 18.4$, $P = 0.001$) (wood mice Mann-Whitney *U* test, year: $z = -3.17$, $P < 0.01$). The effect of age class on intensity was significant in bank voles (GLM, family = negative binomial, age class: $LR_1 = 19.8$, $P = 0.001$) with intensity of helminth infection highest in mature bank voles and lowest in adult bank voles. In wood mice the juvenile age class carried the highest infection intensity with intensity decreasing in adult mice and increasing again in mature hosts, though this was not significant (Kruskal-Wallis test, age

Table 2
Prevalence % (CL_{95}) and mean intensity (±S.E.M) for all helminth species recovered from bank voles by year, age class, site and sex.

	Life cycle (Location)[a]			Prevalence	Intensity
All Helminths		Year	2011	67.7 (57.5–76.7)	22.7 ± 6.0
			2012	93.6 (85.7–97.9)	36.5 ± 5.5
		Age	Juvenile	35.3 (14.2–61.7)	28.2 ± 25.0
			Adult	84.8 (74.4–89.0)	22.9 ± 3.55
			Mature	86.7 (73.2–94.9)	47.2 ± 10.9
		Site	Coole	80.5 (72.4–87.1)	29.6 ± 5.08
			Merlin	75.9 (62.4–86.5)	30.7 ± 6.73
		Sex	Female	73.1 (61.8–82.5)	26.9 ± 4.99
			Male	83.8 (75.1–90.5)	32.0 ± 6.00
		Total		77.4 (72.4–84.8)	29.9 ± 4.09
Aonchotheca murissylvatici	Direct (LI)	Year	2011	29.3 (17.9–36.1)	40.5 ± 14.2
			2012	30.8 (20.8–42.2)	25.2 ± 7.19
		Age	Juvenile	5.90 (0.1–28.7)	5.0 ± NA[b]
			Adult	24.3 (16.8–33.2)	18.8 ± 4.30
			Mature	46.7 (31.7–62.1)	53.6 ± 17.8
		Site	Coole	30.1 (22.1–39.0)	38.9 ± 10.8
			Merlin	24.1 (13.5–37.6)	16.8 ± 4.83
		Sex	Female	25.6 (16.4–36.8)	24.5 ± 9.07
			Male	30.3 (21.5–40.4)	38.9 ± 12.2
		Total		28.2 (21.7–35.5)	33.1 ± 8.15
Aspiculuris tianjinensis	Direct (LI)	Year	2011	51.5 (41.3–61.7)	8.02 ± 2.34
			2012	85.9 (76.2–92.7)	27.2 ± 4.67
		Age	Juvenile	29.4 (10.3–56.0)	32.8 ± 30.0
			Adult	69.6 (60.3–77.8)	17.3 ± 3.50
			Mature	73.3 (58.1–85.4)	20.3 ± 4.68
		Site	Coole	65.1 (55.9–73.4)	17.6 ± 3.34
			Merlin	70.4 (56.4–82.0)	22.8 ± 5.95
		Sex	Female	62.8 (51.1–73.5)	18.9 ± 4.13
			Male	69.7 (59.6–78.5)	18.9 ± 4.16
		Total		66.7 (59.2–73.6)	18.9 ± 2.96
Taenia martis	Indirect (BC)	Year	2011	10.1 (5.0–17.8)	6.10 ± 1.85
			2012	16.7 (9.2–26.8)	18.2 ± 3.64
		Age	Juvenile	0 (0–19.5)	0
			Adult	17.4 (11.0–25.6)	13.3 ± 2.81
			Mature	6.7 (1.4–18.3)	11.0 ± 5.69
		Site	Coole	9.8 (5.1–16.4)	10.5 ± 4.03
			Merlin	20.4 (10.6–33.5)	15.6 ± 2.88
		Sex	Female	10.3 (4.53–19.2)	14.4 ± 5.02
			Male	15.1 (8.74)	12.2 ± 2.91
		Total		13.0 (8.4–18.9)	13.0 ± 2.52

[a] Location within the host is indicated by LI – large intestine; BC- body cavity.
[b] Could not be calculated.

Table 3
Prevalence % (CL_{95}) and mean intensity (±S.E.M) for all helminth species recovered from wood mice by year, age class, site and sex.

	Life cycle (Location)[a]			Prevalence	Intensity
All Helminths		Year	2011	89.8 (82.5–94.8)	44.8 ± 10.1
			2012	97.7 (88.0–99.9)	163.4 ± 57.2
		Age	Juvenile	71.4 (53.7–85.4)	96.3 ± 36.0
			Adult	97.0 (89.6–99.6)	66.4 ± 15.4
			Mature	100 (92.9–100)	92.9 ± 47.3
		Site	Coole	96.4 (91.0–99.0)	97.7 ± 25.3
			Merlin	81.0 (66.9–91.4)	29.7 ± 6.6
		Sex	Female	89.8 (79.2–96.2)	69.6 ± 20.0
			Male	93.5 (86.5–97.6)	88.2 ± 28.7
			Total	92.1 (86.6–95.9)	81.2 ± 19.3
Syphacia stroma	Direct (SI, LI)	Year	2011	74.1 (67.3–81.7)	48.9 ± 12.1
			2012	74.1 (64.8–82.0)	193.9 ± 70.9
		Age	Juvenile	68.6 (50.7–83.1)	100.0 ± 37.4
			Adult	79.1 (67.4–88.1)	75.9 ± 17.9
			Mature	74.0 (59.7–85.4)	110.3 ± 63.6
		Site	Coole	85.5 (77.5–91.5)	102.7 ± 28.2
			Merlin	47.6 (32.0–63.6)	42.7 ± 10.2
		Sex	Female	71.2 (57.9–82.2)	78.6 ± 24.1
			Male	77.4 (67.6–85.4)	100.1 ± 34.4
			Total	75.0 (67.3–81.7)	92.1 ± 23.4
Aonchotheca murissylvatici	Direct (LI)	Year	2011	13.0 (7.27–20.8)	13.5 ± 9.17
			2012	22.7 (11.5–37.8)	5.6 ± 2.05
		Age	Juvenile	0 (0–10.0)	0
			Adult	13.4 (6.33–24.0)	4.78 ± 1.81
			Mature	30.0 (17.9–44.6)	13.5 ± 8.56
		Site	Coole	20.9 (13.7–29.7)	10.6 ± 5.61
			Merlin	2.38 (0–12.6)	2.00 ± NA[b]
		Sex	Female	15.3 (7.22–27.0)	18.7 ± 14.2
			Male	16.1 (9.32–25.2)	5.13 ± 1.65
			Total	15.8 (10.4–22.6)	10.2 ± 5.39
Trichuris muris	Direct (C)	Year	2011	13.9 (7.99–21.9)	1.73 ± 0.30
			2012	13.9 (5.17–27.4)	1.83 ± 0.31
		Age	Juvenile	0 (0–10.0)	0
			Adult	8.96 (3.36–18.5)	1.33 ± 0.33
			Mature	30.0 (17.9–44.6)	1.93 ± 0.28
		Site	Coole	19.1 (12.2–27.7)	1.76 ± 0.23
			Merlin	0 (0–8.40)	0
		Sex	Female	16.9 (8.44–29.0)	1.60 ± 0.34
			Male	11.8 (6.05–20.2	1.91 ± 0.31
			Total	13.8 (8.76–20.3)	1.76 ± 0.23
Taenia martis	Indirect (BC)	Year	2011	0.93 (0–5.05)	3 ± NA[b]
			2012	4.55 (0–15.50	8 ± 0
		Age	Juvenile	2.86 (0–14.90)	3 ± NA[b]
			Adult	1.49 (0–8.03)	8 ± NA[b]
			Mature	2.00 (0–10.6)	8 ± NA[b]
		Site	Coole	2.73 (0–7.75)	6.33 ± 1.67
			Merlin	0 (0–8.410)	0 ± NA[b]
		Sex	Female	1.69 (0–9.09)	8.0 ± NA[b]
			Male	2.15 (0–7.55)	5.5 ± 2.5
			Total	1.97 (0–5.66)	6.33 ± 1.67
Skrjabinotaenia lobata	Indirect (SI)	Year	2011	16.7 (10.2–25.1)	2.44 ± 0.58
			2012	70.4 (54.8–83.2)	6.45 ± 1.17
		Age	Juvenile	2.86 (0–14.9)	3.00 ± NA[b]
			Adult	35.8 (24.5–48.5)	3.38 ± 0.67
			Mature	48.0 (33.7–62.6)	6.67 ± 1.48
		Site	Coole	33.6 (24.9–43.2)	5.59 ± 1.05
			Merlin	28.6 (15.7–44.6)	3.08 ± 6.63
		Sex	Female	27.1 (16.4–40.3)	3.19 ± 0.52
			Male	35.5 (25.8–46.1)	5.85 ± 1.61
			Total	32.2 (24.9–40.32)	4.98 ± 0.82
Hymenolepis hibernia	Indirect (SI)	Year	2011	1.85 (0–6.53)	1.5 ± 0.5
			2012	4.54 (0–15.5)	28.0 ± 27.0
		Age	Juvenile	0 (0–10.0)	0
			Adult	4.48 (0–12.5)	19.3 ± 17.8
			Mature	2.00 (0–10.7)	1.00 ± NA[b]
		Site	Coole	2.73 (0–7.76)	19.0 ± 18.0
			Merlin	2.38 (0–12.6)	2.00 ± NA[b]
		Sex	Female	5.08 (1.06–14.1)	19.0 ± 18.00
			Male	1.07 (0–5.85)	2.00 ± NA[b]
			Total	2.63 (0–6.60)	14.8 ± 13.4
Brachylaemus recurvum	Indirect (SI)	Year	2011	7.40 (3.25–14.1)	2.25 ± 0.65
			2012	11.4 (3.79–24.6)	8.66 ± 6.36
		Age			

Table 3 (*continued*)

	Life cycle (Location)[a]			Prevalence	Intensity
			Juvenile	0 (0–10.0)	0
			Adult	7.46 (2.47–16.6)	1.60 ± 0.40
			Mature	16.0 (7.17–29.1)	6.62 ± 3.95
		Site	Coole	9.09 (4.45–16.1)	5.66 ± 3.20
			Merlin	7.14 (1.50–19.5)	1.67 ± 0.33
		Sex	Female	10.2 (3.82–20.8)	2.50 ± 0.76
			Male	7.53 (3.08–14.9)	6.57 ± 4.59
			Total	8.55 (4.63–14.2)	4.69 ± 2.48
Corrigia vitta	Indirect (PL)			13.8 (8.76–20.3)	9.48 ± 2.18
		Year	2011	11.1 (5.87–18.6)	12.4 ± 3.36
			2012	20.5 (9.80–35.3)	5.56 ± 1.92
		Age	Juvenile	5.71 (0–19.2)	1.00 ± NA[b]
			Adult	17.9 (9.61–29.2)	7.33 ± 1.40
			Mature	14.0 (5.82–26.7)	15.57 ± 5.52
		Site	Coole	6.36 (2.50–12.7)	12.4 ± 5.32
			Merlin	33.3 (19.6–49.5)	8.00 ± 1.98
		Sex	Female	8.47 (2.81–18.7)	14.8 ± 6.51
			Male	17.2 (10.2–26.4)	7.81 ± 2.00

[a] Location within the host is indicated by SI – small intestine; LI – large intestine; C – caecum; BC- body cavity; PL - pancreatic lobes.
[b] Could not be calculated.

class: $\chi^2_2 = 2.94$, $P > 0.05$) (Tables 2 and 3).

Aonchotheca murissylvatici was the most common shared helminth recovered from both hosts. Prevalence of infection was significantly higher in bank voles (GLM, family = binomial, host species: $\chi^2_1 = 6.9$, $P = 0.01$); as was infection intensity (GLM, family = negative binomial, host species: $LR_1 = 16.8$, $P < 0.001$) (Tables 2 and 3). Age class was a significant factor affecting prevalence, with older animals more likely to be infected (GLM, family = binomial, age class: χ^2_2 bank vole = 13.2, $P = 0.001$; wood mice = 12.9, $P = 0.001$). Intensity of infection also increased with age with older animals carrying higher mean burdens (GLM, family = negative binomial, age class: LR_2 bank vole = 10.5, $P < 0.01$; wood mice = 4.84, $P < 0.05$). In wood mice there was a significant difference in prevalence between the 2 sites; the majority of infected hosts occurring in Coole (GLM, family = negative binomial, site: $LR_1 = 4.61$, $P < 0.05$). There was also sex effect on intensity with female wood mice carrying higher worm burdens (GLM, family = negative binomial, sex: $LR_1 = 8.40$, $P < 0.001$) (Table 3).

Prevalence of the shared helminth *Taenia martis* was greater in bank voles (GLM, family = binomial, host species: $\chi^2_1 = 15.6$, $P < 0.01$) (Tables 2 and 3). Infection intensity was also greater in bank voles, however only 3 wood mice in the sample were infected and no further analyses could be done. Adult bank voles had the highest prevalence of *T. martis* with prevalence dropping in mature voles while no voles classified as juvenile were infected (GLM, family = binomial, age class: $\chi^2_2 = 10.9$, $P < 0.001$) (Table 2). More infected bank voles were recovered from the Merlin site (GLM, family = binomial, site: $\chi^2_1 = 5.99$, $P < 0.05$) and infection intensity increased in bank voles in 2012 (GLM, family = negative binomial, year: $LR_1 = 10.5$, $P < 0.01$) (Table 2).

Aspiculuris tianjinensis was found only in bank voles and was the most prevalent parasite of this host (Table 2; Table 4). Infection prevalence increased significantly in 2012 (GLM, family = binomial, year: $\chi^2_1 = 24.2$, $P < 0.001$) with a concurrent increase in intensity of infection (GLM, family = negative binomial, year: $LR_1 = 27.1$, $P < 0.001$). Prevalence also increased through the age classes, reaching the highest prevalence in mature bank voles (GLM, family = binomial, age class: $\chi^2_2 = 10.7$, $P < 0.01$).

A small percentage of bank voles (2.82% CL95 0.09–6.47) carried all 3 helminth species. No wood mice carried all 8 helminth species found in the wood mouse component community. The most species carried by wood mice was 6, which was found in 1 animal (0.65% CL95 0.01–3.61, Fig. 1). The composition of the helminth communities differed in significant ways between bank voles and wood mice. Over half (62%) of helminth species in wood mice had indirect life-cycles, while just 1 helminth species (33%) in bank voles had an indirect-lifecycle (Tables 2 and 3). Mean species richness was higher in wood mice (GLM, family = poisson, host species: $\chi^2_1 = 29.1$, $P < 0.001$) and wood mice had a significantly higher Brillouin's index (GLM, family = quasipoisson, host species: $F_1 = 13.4$, $P < 0.001$) (Table 4).

There were also similarities between the two communities. In both hosts the Berger-Parker Dominance Index showed the helminth component communities were dominated by a directly transmitted nematode species. In bank voles this was by *A. tianjinensis* and in wood mice by *Syphacia stroma* (Table 4). Mean helminth species richness increased in 2012 in both hosts (GLM, family = poisson, year: χ^2_1 bank vole = 7.02, $P < 0.01$; wood mice = 9.26, $P < 0.01$) and mean species richness was greatest in older animals (GLM, family = poisson, age class: χ^2_2 bank vole = 11.5, $P < 0.01$; wood mice = 22.1, $P < 0.001$) (Table 4). Brillouin's index also increased in 2012 in both hosts (GLM, family = quasipoisson, year: F_1, bank vole = 8.96, $P < 0.01$; wood mice = 8.30, $P > 0.01$) and through the age classes (GLM, family = quasipoisson, age class: F_2, bank vole = 8.48, $P < 0.01$; wood mice = 22.5, $P < 0.001$). For bank voles there was also an effect of site with the mean species richness of helminth infracommunities more diverse in Merlin (GLM, family = quasipoisson, site: $F_1 = 5.47$, $P < 0.05$) (Table 4). Simpson's Index was lower in bank voles but this reflects the numerical dominance of one parasite, the nematode *S. stroma* in wood mice samples (Table 4).

4. Discussion

Introduced bank voles in Ireland were found to carry a relatively low number of helminth species, both in comparison to an ecologically similar host living sympatrically with bank voles, and to conspecifics in their native ranges. Across Europe bank voles are known to carry between 3 and 14 helminth species. The lower record from Germany (Klimpel et al., 2007a; Table 5) came from a small sample of animals (29) from an urban setting, which may account for the low species diversity recorded. The present study analysed 177 animals across two years in two sites, and found that bank voles in Ireland are infected with only three helminth species.

The low helminth species diversity in invasive bank voles is

Table 4
Measures of component and infracommunity structure for bank voles and wood mice.

Helminths			Bank vole	Wood mice
Total Species Richness			3	8
Max. Number of Species			3	5
Berger-Parker Dominance Index			0.53	0.92
Dominant Species			*Aspiculuris tianjinensis*	*Syphacia stroma*
Mean Species Richness ±(S.E.M)			1.07 ± 0.05	1.63 ± 0.08
	Year	2011	0.88 ± 0.08	1.39 ± 0.09
		2012	1.33 ± 0.07	2.25 ± 0.16
	Age	Juvenile	0.35 ± 0.12	0.80 ± 0.16
		Adult	1.11 ± 0.07	1.69 ± 0.11
		Mature	1.27 ± 0.11	2.16 ± 0.17
	Site	Coole	1.05 ± 0.06	1.80 ± 0.11
		Merlin	1.15 ± 0.11	1.21 ± 0.13
	Sex	Female	0.99 ± 0.87	1.56 ± 0.14
		Male	1.15 ± 0.07	1.69 ± 0.12
Mean Brillouin's ± (S.E.M)			0.12 ± 0.02	0.17 ± 0.02
	Year	2011	0.07 ± 0.02	0.13 ± 0.02
		2012	0.17 ± 0.03	0.27 ± 0.04
	Age	Juvenile	0	0.01 ± 0.009
		Adult	0.11 ± 0.02	0.16 ± 0.03
		Mature	0.16 ± 0.04	0.30 ± 0.04
	Site	Coole	0.09 ± 0.02	0.19 ± 0.03
		Merlin	0.17 ± 0.03	0.12 ± 0.03
	Sex	Female	0.10 ± 0.02	0.15 ± 0.03
		Male	0.13 ± 0.02	0.19 ± 0.03
Max Brillouin's			0.86	1.19
Simpson's Index			0.55	0.44

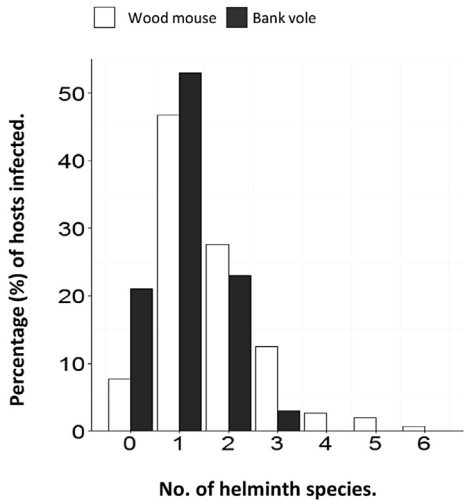

Fig. 1. Frequency distribution of intestinal helminth species richness in wood mice and bank voles examined in 2011 and 2012.

likely due to both the loss of indigenous helminths during translocation and establishment and the lack of native helminths acquired from hosts in Ireland. For example, bank voles in Europe are often infected with *Heligmosomum mixtum* (Behnke et al., 2008; Bjelić-Čabrilo et al., 2011) but this parasite was never recorded in bank voles in Ireland. *Heligmosomum mixtum* may have been absent from the founder population or failed to establish. The haplotype diversity of Irish bank voles indicates that the founder population was small, or went through a population bottleneck during range expansion (Stuart et al., 2007). As host sample size is correlated with parasite species richness, and due to the overdispersed nature of parasites, small founder populations will host only a proportion of the parasites found in the original parasite community (Walther et al., 1995; Shaw et al., 1998). Parasites that do occur in the founder population may be lost during the establishment and range expansion phases of species invasions. Epidemiological models suggest there is a host threshold density below which a parasite cannot sustain itself (Anderson and May 1979) and many co-introduced parasites will go extinct before the required threshold densities for parasite maintenance can be reached (Torchin et al., 2003; Colautti et al., 2004).

Finally, opportunities for bank voles to encounter new helminth species in Ireland are limited with no other arvicoline species present and only three ground-dwelling rodent species occurring (Marnell et al., 2009; Montgomery et al., 2014). Similarly, Gozzi et al. (2014) suggest the low species diversity of intestinal helminths in the invasive red-bellied squirrel (*Callosciurus erythraeus*) in Argentina may be due to the lack of sympatric sciurid rodents and scarcity of ecologically similar (arboreal) mammals. Introduced species can, however, acquire novel parasites if native hosts carry generalist parasites with low-host specificity, particularly if host share similar ecological characteristics (Barton, 1997; Pisanu et al., 2007, 2009).

All three helminths recorded in Irish bank voles may have co-invaded along with the bank vole as opposed to have been acquired in Ireland. *Aspiculuris tianjinensis* is the strongest candidate for co-invasion. *Aspiculuris tianjinensis* has not been recorded in wood mice in Ireland either in this study, or in previous studies (Langley and Fairley, 1982; O'Sullivan et al., 1984; Montgomery and Montgomery, 1989) but has been recorded in bank voles in their native range (Grzybek et al., 2015). *Aspiculuris tianjinensis* has recently been shown to be a different species to that parasitizing house mice, *Aspiculuris tetraptera* (Behnke, 1975; Behnke et al., 2015).

The cestode *T. martis* requires two host species to complete its lifecycle. Intermediate hosts include a variety of rodent species (Klimpel et al., 2007a; Loos-Frank and Zeyhle, 1982) and definitive hosts in Europe include badgers (*Meles meles*) and foxes (*Vulpes vulpes*) (Loos-Frank and Zeyhle, 1982). As both badgers and foxes are found in Ireland (Montgomery et al., 2014), either or both of these species may act as the definitive host for *T. martis* enabling its establishment in Ireland. To date *T. martis* has not been recorded in general parasitological surveys of foxes and badgers (Ross and

Table 5
Prevalence (%) and mean intensity/abundance (in brackets) of intestinal helminth parasites in bank voles throughout their native range in Europe.

Location	Sample size	All helminths	Total species[a]	Reference[b]
Ireland	177	77.4% (29.9[c]) (23.7[d])	3	Present study
Southern Norway	398	29.4% (3.2[c])	8	Tenora et al., 1979
Poland (3 sites)	40	95% (109.9[d])	9	Behnke et al., 2001
	41	68.3% (129.9[d])	6	
	58	91.4% (16.1[d])	9	
Germany	29	69.0% (26.2[d])	3	Klimpel et al., 2007a
Poland (3 sites)	112	89.3% (52.1[d])	13	Behnke et al., 2008
	114	73.8% (52.3[d])	10	
	132	81.1% (12.9[d])	10	
Spain (2 sites)	271	72.3%	14	Ribas et al., 2009
	105	51.42%	10	
Serbia	588	Nematodes 60.2% (20.8[c]) Cestodes 20.7% (3.67[c])	14	Bjelić-Čabrilo et al., 2011
Poland (3 sites)	304	85.% (23.8[d])	–	Grzybek et al., 2015
	209	77.9% (31.8[d])	–	
	328	75.0% (10.0[d])	–	

[a] Total species includes juvenile and adult cestodes.
[b] References are listed according to the date the study was under taken.
[c] Intensity.
[d] Abundance.

Fairley, 1969; Stuart et al., 2013) though in Wolfe et al. (2001) the *Taenia* recovered were too degraded to identify to species level.

While the requirement for more than one host species can reduce the likelihood of an introduced parasite establishing in a new environment (Torchin and Mitchell, 2004), helminths with indirect life cycles can become established if they have a wide host specificity (Kennedy, 1993) and a recent literature review of the topic showed a number of parasites with indirect life cycles do co-invade (Lymbery et al., 2014). *Taenia martis* was recorded in wood mice in this study but has not been recorded in previous studies of wood mice in Ireland (Langley and Fairley, 1982; O'Sullivan et al., 1984; Montgomery and Montgomery, 1989), nor was it recorded in wood mouse populations in Ireland sampled concurrently in sites beyond the invasion front of bank voles (K. C. Loxton unpublished data). To our knowledge this is the first recording of *T. martis* in small rodents in Ireland. *Taenia martis* is regularly recorded in bank voles in Europe (Behnke et al., 2008; Grzybek et al., 2015). Additionally, the greater prevalence and intensity of *T. martis* in bank voles and lack of records for this helminth in Irish wood mice suggest that bank voles are acting as a reservoir for *T. martis* infection which is spilling over to wood mice.

The final helminth recorded in bank voles in Ireland, *A. murissylvatici,* was recorded in wood mice in the present study as well as in previous studies on wood mice carried out in sites beyond the invasion front of the bank vole in Ireland (Montgomery and Montgomery, 1989). Therefore, unlike *A. tianjinensis* and *T. martis* there is evidence for *A. murissylvatici* existing in Ireland prior to the introduction of the bank vole. As such, the possibility that *A. murissylvatici* may have been acquired by bank voles after establishment in Ireland is more difficult to rule out. *Aonchotheca murissylvatici* is a common nematode of both murid and arvicolid rodents, having a wide host range in these groups (Montgomery and Montgomery, 1989; Justine and de Roguin, 1990; Milazzo et al., 2003; Klimpel et al., 2007a, 2007b; Bjelić-Čabrilo et al., 2011) as well as in more distantly related rodents (Pisanu et al., 2009). Parasitological surveys in Europe and Ireland record *A. murissylvatici* having a lower prevalence and intensity in wood mice than bank voles, suggesting bank voles are the more competent host (O'Sullivan et al., 1984; Pisanu et al., 2009). The present study found similar results; both prevalence and abundance of *A. murissylvatici* was significantly higher in bank voles.

Parasites with indirect life-cycles will not be able to co-invade along with invasive hosts if their intermediate or definitive hosts are missing in the invaded habitat, or if environmental conditions are unsuitable for free-living stages (Torchin and Mitchell, 2004; Thieltges et al., 2008). The low numbers of helminth species with indirect life-cycles in invasive bank voles in Ireland reflects this.

Low parasite diversity in introduced hosts has been suggested as an explanation for the success of invasive species. The Enemy Release Hypothesis posits that a decrease in regulation by natural enemies (including parasites) results in an increase in distribution and abundance of invading hosts (Torchin et al., 2003; Torchin and Mitchell, 2004; Keane and Crawley, 2002). In Ireland Montgomery et al. (2012) found that the presence of the bank vole affected the abundance of the wood mice negatively. In the present study we found that while both shared parasites have a higher prevalence in bank voles, overall helminth intensity and abundance is higher in wood mice, which has also been found in populations where both species are considered native (Lewis and Twigg, 1972).

The effects of release from parasites or lower parasite prevalence and abundance will depend on the virulence of each particular helminth species, which is often complicated by number of biotic and abiotic interactions such as food supply (Pedersen and Greives, 2008). However the detrimental effects of helminth parasites not only increase with parasite burden, but with diversity of parasites species too. Increasing helminth species richness has been associated with lower levels of abdominal fat and host body mass (Lello et al., 2005), increased immune investment (Bordes and Morand, 2011) and more severe disease outcomes than expected from single infections (Ezeamama et al., 2008). The overall lower parasite prevalence and intensity and lower species diversity found in invasive bank voles may be part of the explanation for the replacement of the wood mouse by the bank vole found by Montgomery et al. (2012). However, a more complete parasitological survey is required to determine if the trend toward reduced parasitism seen in helminths in this study is also present in other parasite groups.

Conflict of interest statement

The authors declare that there is no conflict of interest.

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