Disruption of a host-parasite system following the introduction of an exotic host species

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SUMMARY

The potential of biological invasions to threaten native ecosystems is well recognized. Here we describe how an introduced species impacts on native host-parasite dynamics by acting as an alternative host. By sampling sites across an invasion front in Ireland, we quantified the influence of the introduced bank vole (*Clethrionomys glareolus*) on the epidemiology of infections caused by flea-transmitted haemoparasites of the genus *Bartonella* in native wood mice (*Apodemus sylvaticus*). *Bartonella* infections were detected on either side of the front but occurred exclusively in wood mice, despite being highly prevalent in both rodent species elsewhere in Europe. Bank vole introduction has, however, affected the wood mouse-*Bartonella* interaction, with the infection prevalence of both *Bartonella birtlesii* and *Bartonella taylorii* declining significantly with increasing bank vole density. Whilst flea prevalence in wood mice increases with wood mouse density in areas without bank voles, no such relationship is detected in invaded areas. The results are consistent with the dilution effect hypothesis. This predicts that for vector-transmitted parasites, the presence of less competent host species may reduce infection prevalence in the principal host. In addition we found a negative relationship between *B. birtlesii* and *B. taylorii* prevalences, indicating that these two microparasites may compete within hosts.

Key words: introduced species, reservoir competence, density-dependent transmission, host specificity, Siphonaptera, vector, dilution effect.

INTRODUCTION

Biotic invasions are recognized as major agents of global change with the potential to disrupt native ecosystems and inflict environmental damage (Mack *et al*. 2000). Interactions between introduced and native species can be mediated through a range of processes, including parasitism and disease. The direct threat of exotic parasites to native populations is well established (Dobson & Foufopoulos, 2001), and there has been much recent emphasis on the potential for parasites to influence the ability of an exotic species to invade (Mitchell & Power, 2003; Torchin *et al*. 2003). However, far less attention has been devoted to the capacity of introduced parasites or hosts to perturb established host-parasite systems. As theoretical predictions that parasites and disease can play an important role in host dynamics (Tompkins *et al*. 2002) gain increasing empirical support (Hudson, Dobson & Newborn, 1998; Telfer *et al*. 2002), it is becoming clear that such perturbations could have profound consequences.

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Host community structure can fundamentally influence the establishment and prevalence of shared parasites (Holt *et al*. 2003). The arrival of an alternative host could result in an increase in abundance of a native parasite, thereby potentially reducing the population growth rate of susceptible hosts (Holt & Lawton, 1993). Such 'apparent competition' between host species can result in the extinction of the host suffering the greatest negative impact of the shared parasite (Holt & Lawton, 1993). Conversely, the 'dilution effect' predicts that for vector-transmitted parasites, or those with a free-living infectious stage, the presence of species with reduced host competence may reduce infection prevalence in the principal host, because infections are transmitted to the less competent species that would otherwise be transmitted to the principal host (Norman *et al*. 1999; Ostfeld & Keesing, 2000*a*, *b*).

Despite the potentially important role of parasites in invasions, there have been relatively few empirical studies. In a review of parasites in a range of introduced animal species, data for several host taxa had to be restricted to parasitic helminths (Torchin *et al*. 2003). Invasion fronts represent a unique opportunity to investigate the ecology of introduced species, and have been used successfully before to examine factors influencing the spread of three alien

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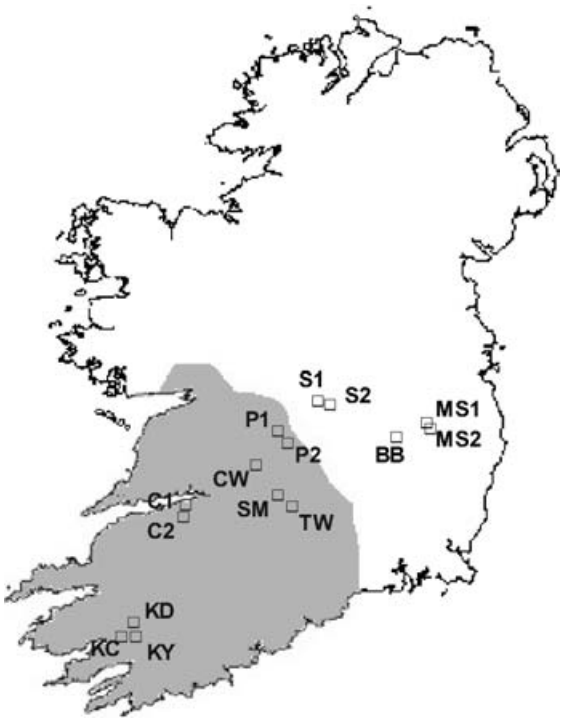

Fig. 1. Map of Ireland showing the distribution of sampling sites. The shaded region indicates the area estimated to be inhabited by bank voles at the end of December 2002 (T. Hayden, unpublished data).

oak gall wasps (Walker, Leather & Crawley, 2002). However, to our knowledge no study has previously used an invasion front to examine the impact of an introduced species on native host-parasite systems.

We examined the impact of the introduced *Clethrionomys glareolus* Schreber (bank vole) on the epidemiology of *Bartonella* species (flea-transmitted haemotrophic bacteria) in woodland rodent populations in Ireland. A small founder population of bank voles was introduced to the south-west of Ireland between 1945 and 1960 and has subsequently spread at an estimated 2–4·5 km/year (Smal & Fairley, 1984). In invaded areas, bank voles are sympatric with *Apodemus sylaticus* L. (wood mice), Ireland's only native small woodland rodent. In Britain, where wood mice and bank voles commonly live in sympatry, they are known to share several microparasites, including up to 5 species of *Bartonella* (Birtles *et al*. 2001).

MATERIALS AND METHODS

Study sites

Fifteen sites in mixed woodland were trapped in November 2002, of which 5 were ahead of the invasion front (Fig. 1). The distance between sites ranged from 3·2 to 344·5 km, apart from 2 sites which were separated by less than 100 m. Data from these two sites were combined in analyses. Each site was trapped using a 5×5 grid of uglan special mouse traps, set at 15 m intervals. Traps were pre-baited with whole-wheat grain and carrot for 1 night and then set for 2 nights, with traps checked daily. On capture, sex, reproductive condition and weight were recorded. Animals were assigned to one of three age categories (juvenile 2–6 weeks old, subadult 6–10 weeks old and adult >10 weeks old) on the basis of weight (Telfer *et al*. 2002). Females were defined as mature if they had a perforate vagina, open pubic symphysis or enlarged nipples. Males were defined as mature if they had descended testes. The presence of fleas was recorded. All captured animals were humanely killed and a blood sample taken by cardiac puncture. Bodies were stored in separate bags and frozen. Sera were separated from the blood samples by centrifugation. Red cell pellet samples were stored at −80 °C.

Identification of Bartonella *in rodents and fleas*

A 50 μl aliquot of each sample was plated onto 10% (v/v) sheep blood-enriched Columbia agar. Plates were incubated at 35 °C and 5% CO_2 for up to 45 days. Plates were checked daily for bacterial growth, and colonies tentatively identified as bartonellae (small, round, grey-white colonies) were passaged onto clean plates. After 1 week's growth, isolates were harvested into brain heart infusion broth containing 10% glycerol for frozen storage. A sweep of colonies from each primary isolation plate was harvested into sterile, distilled water for use as template in polymerase chain reaction (PCR)-based identification assays (see below). If there were less than 100 colonies all colonies were harvested. If more than 100 colonies were present or *Bartonella* growth resembled a lawn, a representative sweep of colonies was harvested.

Fleas collected following brushing of the rodent body with a fine comb in the laboratory were identified to species using a taxonomic key (Smit, 1957) and then stored in individual tubes containing 70% ethanol. DNA extracts were prepared from fleas by alkaline digestion (Bown *et al*. 2003).

Bartonella DNA was detected in bacterial cell suspensions using a *Bartonella* genus-specific PCR assay that amplifies a fragment of the 16S–23S intergenic spacer region (ISR). Each reaction mixture comprised 15 μl of $2 \times$ PCR mastermix (Abgene), 0·2 μl of a 100 μmol/μl solution of primer big-F (5′-TTG ATA AGC GTG AGG TC), 0·2 μl of a100 μmol/μl solution of primer big-R (5′-TCC CAG CTG AGC TAC G), 13·6 μl sterile, distilled water and 1 μl of bacterial cell suspension. Reaction mixtures were exposed to a thermal cycle consisting of 96 °C for 3 min followed by 40 cycles of 96 °C for 10 sec, 55 °C for 10 sec and 72 °C for 50 sec. *Bartonella* DNA was detected in DNA extracts prepared from fleas using a semi-nested PCR assay. In this approach, the PCR described above was used

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as a second round reaction and was preceded by a first round reaction in which primer big-R was replaced with primer bog-R (5′-TGC AAA GCA GGT GCT CTC CCA). The first round reaction mixture was subjected to the thermal cycle described above, and then 1μl of this reaction mix was used in the second round reaction. The use of PCRs targeting the ISR exploits recognized inter-*Bartonella* species hypervariability such that amplification products derived from different *Bartonella* species are of different sizes (Roux & Raoult, 1995). Electrophoretic resolution of PCR products on 3% (w/v) agarose gels ('Hi-Pure' Low EEO, BioGene, Cambridgeshire) stained with ethidium bromide and visualized using UV light permitted identification of the *Bartonella* species.

Statistical analyses

We investigated what factors influence the probability that an individual animal is (a) infected with a *Bartonella* sp. and (b) infested with fleas. Data for the two host species and the different *Bartonella* species were analysed separately. There was a close association between the presence and absence of fleas recorded in the field and laboratory ($\chi^2_1 = 28{\cdot}01$, $P < 0{\cdot}001$), and animals were scored as having fleas if they had fleas recorded by either method. However, as some individuals were scored as having fleas in the field but not in the laboratory it was not possible to analyse different flea species separately. As early studies of *Bartonella* in Germany found no evidence of vector specificity, with a tropical rat flea successfully transmitting German strains between hosts (Krampitz, 1962), overall flea prevalence, rather than prevalence of a specific flea species, is predicted to influence *Bartonella* dynamics.

Initially we included individual level covariates (sex, age class, maturity and presence of fleas (for the *Bartonella* analyses) with up to two-way interactions) in generalized linear mixed models (GLMMs), with a logit link, binomial errors and site as a random effect. Where one or more individual covariates were found to have a significant effect, the effects of population level covariates were investigated using GLMMs incorporating the significant individual covariates, plus site as a random effect. If no individual covariates were found to have an effect, population level covariates were investigated using generalized linear modelling (GLM), with the proportion of infected or infested animals at a site as the response variable. The population level covariates investigated were bank vole density, wood mouse density, total rodent density (for the flea analyses), and, in wood mouse analyses, 'bank vole presence', a binary variable describing whether a site was behind or ahead of the invasion front. Interactions between bank vole presence and wood mouse density were also investigated. Density was the number of animals caught in the 0·36 ha grid over 2 days. For the two grids that were combined for analyses, the median number caught was used. In addition, we investigated interactions between *Bartonella* species by including the prevalence of other *Bartonella* species as a population level covariate. For analyses without random effects, model selection was based on Akaike Information Criterion (AIC), which aims to find the simplest model that adequately explains the data (see Johnson & Omland, 2004 for review of model selection approaches). A difference in AIC of 2 can be considered significant (Burnham & Anderson, 1992). In the absence of model selection criteria such as AIC for GLMM, for analyses with random effects we conducted a backward stepwise selection procedure, retaining only terms significant ($P < 0{\cdot}05$) based on the *t*-tests for the parameter coefficients.

RESULTS

A total of 120 wood mice were caught from the 15 sites (range = 3–17), whilst 104 bank voles were caught (range = 0–17) from the 10 sites behind the invasion front (Fig. 2A). Behind the front there was no correlation between the numbers of bank voles and wood mice caught (r = 0·18). Due to contamination and overgrowth on the plates, assessment of *Bartonella* infection status by isolation was not possible for 11 bank voles and 16 wood mice. Although 50% (52/104) of wood mice were infected with *Bartonella*, no bank vole was infected (0/93). *Bartonella* were identified to species for all infected animals. There was 1 mixed infection; hence 53 isolates were identified. Three species were encountered, with 23 isolates (43%) identified as *Bartonella birtlesii*, 29 isolates (55%) identified as *Bartonella taylorii*, and 1 isolate (2%) identified as a *Bartonella doshiae*-like strain (wbs011) that had previously been encountered in wood mice and bank voles in the UK (Birtles *et al*. 2001). The prevalence of *B. taylorii* and *B. birtlesii* in wood mice varied between sites from 0% to 75% (Fig. 2B). Five of the 11 sites with *Bartonella*-infected animals had both *B. birtlesii* and *B. taylorii* species present. The single mixed infection detected involved *B. birtlesii* and the *Bartonella doshiae*-like strain (wbs011). No mixed infections of *B. birtlesii* and *B. taylorii* were recorded.

Overall 35% of bank voles and 12% of wood mice were infested with fleas. In the laboratory, we obtained 31 *Amalaraeus penicilliger* Dale from 10 individuals, 30 *Ctenophthalmus nobilis* Rothschild from 19 individuals and 12 *Hystrichopsylla talpae* Curtis from 11 individuals. The prevalences of each flea species on the two host species varied, with 3·2% of the *A. penicilliger*, 37% of the *C. nobilis* and 25% of the *H. talpae* found on wood mice. *Bartonella* DNA was detected by PCR in 13 out of 69 fleas (19%), 12 of which were *C. nobilis* and one *A. penicilliger*. Six bank

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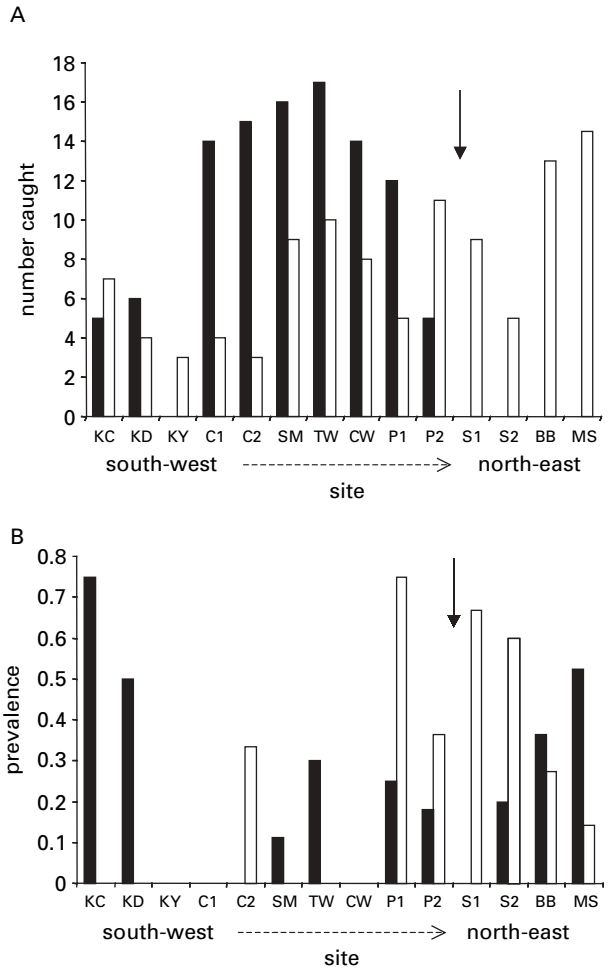

Fig. 2. (A) The number of each species caught at each site. Site codes refer to Fig.1. The solid arrow indicates the current position of the invasion front. The number caught at MS represents the median of MS1 and MS2 as the two grids were separated by less than 100 m. Filled bars indicate bank voles, open bars indicate wood mice. (B) The prevalence of *Bartonella* infections in wood mice. Filled bars indicate *B. taylorii*, open bars indicate *B. birtlesii*.

voles and 5 wood mice had fleas that were PCR positive for *Bartonella* DNA feeding on them, and 2 of these wood mice were bacteraemic with *Bartonella*.

Bartonella *infections in wood mice*

Analyses were conducted for the two common species, *B. birtlesii* and *B. taylorii*. The best model was similar for both species. The probability of a wood mouse being infected was not related to sex, age, maturity or the presence of fleas for either *B. birtlesii* or *B. taylorii*. The proportion of wood mice infected with *B. birtlesii* decreased with increasing prevalence of *B. taylorii* and increasing bank vole density (Table 1; odds ratios: *B. taylorii* prevalence = 0·08 (95% C.I. 0·007–0·85), bank vole density = 0·87 (95% C.I. 0·79–0·95)), whilst the proportion of wood mice infected with *B. taylorii* decreased with increasing prevalence of *B. birtlesii* and increasing bank vole density (Table 1; odds ratios: *B. birtlesii* prevalence = 0·06 (95% C.I. 0·004–0·95), bank vole density = 0·89 (95% C.I. 0·82–0·97)). Although the addition of wood mouse density to the best model for *B. taylorii* resulted in a drop in the model deviance, the improvement in fit was insufficient to be significant based on AIC values ($\Delta AIC = +0{\cdot}08$). For both species, models that included bank vole density as an explanatory variable, rather than bank vole presence were marginally better ($1 < \Delta AIC < 2$).

Flea infestations in wood mice and bank voles

Again, the probability of a wood mouse being infested with fleas was not related to sex, age or maturity. At the population level, the best model had an interaction between bank vole presence and wood mouse density (Table 1), such that in the area invaded by bank voles the proportion of wood mice infested with fleas decreased with wood mouse density, but ahead of the invasion front there was an increase in flea prevalence with wood mouse density (Fig. 3; parameter estimates on logit scale (S.E.): intercept −1·93 (1·59); wood mouse density −0·20 (0·19); bank vole presence 3·34 (1·59); wood mouse density * bank vole presence −0·49 (0·19)).

Male bank voles were more likely to be infested with fleas than females (odds ratio = 3·21 (95% C.I. 1·15–8·94); $t = 2{\cdot}24$, $P = 0{\cdot}025$). No population level covariate improved the fit of the GLMM. The variance contributed by the site level effect was 1·03 (S.E. = 0·64).

DISCUSSION

Given that no infections were detected in bank voles, *Bartonella* species appear not to have accompanied bank voles to Ireland. Moreover, it seems that bank voles are not infected with the *Bartonella* species already present in Ireland. We have considered three possible explanations. Firstly, infections are present in bank voles but at very low prevalence. If overall *Bartonella* prevalence was less than 3%, the probability of obtaining no positive samples out of 93 is greater than 0·05 under a binomial distribution. However, surveys of rodents from Britain and elsewhere suggest prevalences for all *Bartonella* species combined are typically high (Birtles, Harrison & Molyneux, 1994; Kosoy *et al.* 1997). At a mixed woodland study site in northwest England, the observed prevalence in bank voles in autumn has consistently been >25% (S. Telfer and R. Birtles, unpublished data; $n = 188$). Thus, *Bartonella* is either absent from Irish populations of bank voles or at an atypically low prevalence.

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Table 1. Model selection for GLM of the proportion of wood mice (A) infected with *Bartonella birtlesii*, (B) infected with *B. taylorii* and (C) infested with fleas

(All combinations of variables were considered, but only the best 4 models are shown, with the best model in bold. ΔAIC is the difference in AIC between a model and the best model. np = number of parameters, bv = bank vole, wm = wood mouse.)

Model	Deviance	np	AIC	ΔAIC
(A) *B. birtlesii*				
***B. taylorii* + bv density**	**97·91**	**3**	**103·91**	
B. taylorii + bv presence	99·68	3	105·68	1·77
B. taylorii + bv density + wm density	97·91	4	105·91	2·00
bv density	102·61	2	106·61	2·70
(B) *B. taylorii*				
***B. birtlesii* + bv density**	**113·57**	**3**	**119·57**	
B. birtlesii + bv density + wm density	111·65	4	119·65	0·08
B. birtlesii + bv presence	115·06	3	121·06	1·49
B. birtlesii + bv presence + wm density	114·09	4	122·09	2·52
(C) Fleas				
Wm density * bv presence	**75·68**	**4**	**83·68**	
bv presence	87·65	2	91·65	7·97
wm density	89·57	2	93·57	9·89
wm density + bv area	87·59	3	93·59	9·91

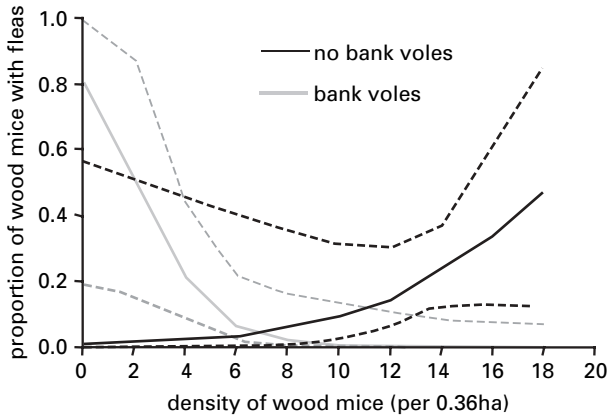

Fig. 3. Based on the best model from Table 2A, the predicted relationship between wood mouse density and the proportion of wood mice with fleas, for areas with and without bank voles. Dashed lines indicate the 95% confidence limits.

The second possibility is that opportunities for transmission do not exist. However, as bank voles and wood mice were found to share flea species and fleas containing *Bartonella* DNA were collected from bank voles, this explanation appears unlikely.

Thirdly, and most plausibly, the introduced bank voles are not susceptible to the native *Bartonella* strains, because of differences in either the parasite or the host compared to other studies. The particular *Bartonella* strains present in Ireland may not be able to exploit bank voles; alternatively the Irish bank voles may be innately resistant to bartonellae. All three of the *Bartonella* species we encountered in Irish wood mice infect wood mice and bank voles in the UK, with bank voles serving as significant hosts for both *B. birtlesii* and *B. taylorii* in north-west England (Birtles *et al*. 2001). However, although the *Bartonella* species and strains present in the UK can infect several rodent species, there is experimental evidence that some rodent-associated *Bartonella* strains may be more host-specific. A study in the USA that examined the ability of different *Bartonella* species and strains to infect different rodent species found that only animals inoculated with strains originally obtained from the same or a phylogenetically closely related species developed bacteraemia (Kosoy *et al*. 2000). Similarly, in early studies in Germany there was some suggestion of *Bartonella* host specificity within wood mouse and bank vole communities (Krampitz & Kleinschmidt, 1960; Krampitz, 1962). Both the origins of Irish wood mice and their parasitic fauna, and the origin of Irish bank voles remain unknown. The capacity of *Bartonella* species and strains to infect bank voles has only been demonstrated in Germany, Norway, the UK, Sweden and Poland (Krampitz, 1962; Wiger, 1979; Birtles *et al*. 1994; Bajer *et al*. 2001; Holmberg *et al*. 2003). Until populations from elsewhere are sampled, the distribution of bank vole-associated bartonellosis remains unresolved.

Although the *Bartonella* species present in Ireland do not appear to infect bank voles, the introduction of bank voles has had a significant effect on wood mouse-*Bartonella* interactions, for both species of *Bartonella*, reducing the infection prevalence at sites with high-density bank vole populations. The results are consistent with the dilution effect hypothesis for vector-borne parasites, which predicts that high

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species diversity in the community of vector hosts reduces vector infection prevalence by reducing the contact rate between the vector and the most competent parasite reservoir (Norman *et al*. 1999; Ostfeld & Keesing, 2000*a*, *b*; see also Holt *et al*. 2003). The dilution potential of a species depends on both its typical density and its reservoir competence (LoGiudice *et al*. 2003). The present system includes generalist vectors in which parasite transmission is (probably) exclusively horizontal, and vertebrates exhibiting profound variation in reservoir competence, including a 'dilution host' (the bank vole) with high flea burden and low (or no) reservoir competence. Hence, this system does indeed fulfil the criteria described by Ostfeld & Keesing (2000*a*) as being necessary for the dilution effect.

The extent to which the dilution effect will reduce the prevalence of a vector-borne parasite will also depend, however, on how the abundance of the vector changes with host species diversity. If an increase in diversity is accompanied by an increase in the total number of hosts and a corresponding increase in vector population size, then the dilution effect may be prevented, as long as the number of host-vector-host contacts between competent hosts is not reduced. In the present study, however, although flea prevalence on wood mice increased with wood mouse density in areas without bank voles, in invaded areas flea prevalence on neither wood mice nor bank voles was related to total rodent density. These results suggest that although flea dynamics may be influenced by host availability, the fleas do not show a simple response to sympatric populations of bank voles and wood mice as a single host resource. At low wood mouse densities, the presence of bank voles increased the prevalence of fleas on wood mice relative to non-invaded areas. However, at high wood mouse densities flea prevalence on wood mice is reduced in invaded areas compared to non-invaded areas, presumably as a result of a dilution effect. Although the analyses of flea prevalence need to be interpreted with caution as different flea species had to be combined, the results are entirely consistent with the dilution effect hypothesis for vector-borne parasites. Combined with the low reservoir competence of bank voles for *Bartonella*, the dilution effect on flea prevalence leads to a very strong dilution effect on *Bartonella* prevalence at high bank vole densities. Complex effects of relative host density on parasite prevalence have also been shown by both empirical and modelling studies of the *Ixodes ricinus*-louping ill virus system in Scotland (Laurenson *et al*. 2003).

The observed negative interaction between the two commonest *Bartonella* species indicates that within a single site either *B. birtlesii* or *B. taylorii* tends to dominate. There are three potential explanations. First, if species differ in their typical intensity of infection within hosts, or in their growth rates on plates, then mixed infections may be underestimated, and a site with a low prevalence of the species preferentially detected might appear to have an unusually high prevalence of the second species. Although there is no obvious difference between *Bartonella* species in their growth rate on plates (R. Birtles, unpublished data), examination of blood smears taken during this study showed that the intensity of *B. taylorii* infections tended to be greater than *B. birtlesii* infections (median number of red blood cells infected: *B. taylorii* = 5·59 per 100 000 cells ($n = 13$), *B. birtlesii* = 0·12 per 100 000 cells ($n = 19$); Kruskall-Wallis test, $P = 0{\cdot}05$). However, a difference in the intensity of infection of only a single order of magnitude seems unlikely to fully explain the lack of mixed infections.

A second possibility is that environmental conditions may favour different *Bartonella* species at different sites. If flea species differ in their vector competence, one such difference could be differences in the flea community. There was no obvious difference in the distribution of the 2 commonest flea species, with both recorded from 6 of the 7 sites that had fleas identified to species from at least 2 animals. All individuals of the third species recorded (*Amalaraeus penicilliger*) were obtained from a single site. As *A. penicilliger* is predominantly a bank vole flea (Smit, 1957) it is likely that it was introduced into Ireland with the bank vole.

Lastly, the result may suggest that competition is occurring between *B. birtlesii* and *B. taylorii*. Interactions between concomitant parasites have long been recognized, but have been the subject of only limited study (reviewed by Cox, 2001), and competition between gut helminths within individual animals has recently been reported in a study of a wild population of rabbits (Lello *et al*. 2004). Similar competition between bartonellae within individual hosts could lead to the differences in site level prevalence observed in this study. No mixed infections of *B. birtlesii* and *B. taylorii* were recorded, despite both species being relatively common and co-occurring in 5 sites. Further work is required to investigate interspecific competition.

Changes to flea and *Bartonella* prevalence may have consequences for wood mice fitness and population dynamics. Parasitism by fleas can result in reduced body mass (Khokhlova *et al*. 2002) and fecundity (Neuhaus, 2003). Although *Bartonella* infections are generally thought to be asymptomatic in their reservoir hosts (Chomel *et al*. 2003), laboratory mice infected with *B. birtlesii* are more likely to have failed pregnancies and produce smaller viable fetuses (Boulouis *et al*. 2001). Changes in flea prevalence could also impact on other flea-transmitted microparasites, such as trypanosomes. Moreover, the introduction of bank voles may have also influenced the distribution and number of ticks

and thus the parasites they transmit. Such predictions are currently under investigation.

This study indicates that the introduction of the bank vole has had a significant impact on wood mouse-*Bartonella* dynamics. The data presented are correlative and represent a single time-period. Consequently, several explanations are possible, including variation in habitat or climate between sites or changes in wood mouse behaviour. However, given the effect of bank voles on flea prevalence, the dilution effect seems the most parsimonious explanation. Thus, this study may be the first demonstration that the introduction of an exotic host species can affect native host-parasite dynamics through the dilution effect and demonstrates that introduced species may initiate significant effects on host-parasite systems. As the introduction of a single host species has the potential to influence a large number of different parasites, the impact on population dynamics and ecosystems may be considerable. The study also highlights the insights that can be obtained from studying host-parasite dynamics across an invasion front.

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