Migratory passerine birds in Britain can carry *Phytophthora ramorum* inoculum on their feathers and "feet" at low frequency.

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SUMMARY

In this study we investigated whether birds could be vectors facilitating long-distance spread of *Phytophthora ramorum* in Britain. Migratory bird species associated with the main sporangium-producing host plants and most likely to pick up *P. ramorum* spores were considered. Swabs were taken from the flank and 'feet' of 1,014 birds over a twelve month period (April 2011 to March 2012) in the west of Britain, and subsequently analysed for the presence of *P. ramorum* using nested PCR. Ten positive samples from 10 birds were identified: three in Cornwall, one in Devon, three in Gloucestershire, two in north Wales and one in Merseyside. *Phytophthora ramorum* was detected on samples from four species of thrushes (Redwing *Turdus iliacus*, Fieldfare *Turdus pilaris*, Blackbird *Turdus merula* and Song Thrush *Turdus philomelos*) and one species of warbler (Chiffchaff *Phylloscopus collybita*). All birds that tested positive were sampled in late autumn and winter (October-February), when long-distance movements (over 100km) would have stopped. The low incidence of *P. ramorum* found using PCR suggests that the incidence of inoculum, whether viable or not, on birds was low. The apparently low incidence of inoculum on birds and timing of positive

samples suggest migratory passerine birds can carry *P. ramorum* inoculum on their feathers and "feet", albeit at low frequency.

1 | INTRODUCTION

Phytophthora ramorum is an oomycete, a class of eukaryotic micro-organisms that includes species known to be among the most pathogenic to plants. Asexual sporulation occurs on foliage of infected plants either as sporangia, which are involved in rapid reproduction and in the rapid spread of the disease during an epidemic, or chlamydospores, which are resting spores that can survive adverse environmental conditions better than sporangia (Grünwald et al. 2012). Therefore, foliar hosts (e.g. *Rhododendron* spp.) are important in the spread of the pathogen, although not all infected hosts die from the infection (Anacker et al. 2007; Davidson et al. 2003; Di Leo et al. 2009).

P. ramorum was found in Great Britain for the first time in 2002 in a garden centre in West Sussex, since when it has been recorded on many ornamental plant species, *Rhododendron* spp. and *Viburnum* spp. and heathland plants such as *Vaccinium myrtillus* (Defra 2009; Forestry Commission 2017). Affected plants were found to grow mostly in the proximity of infected *Rhododendron* spp. (Forestry Commission 2017; Scottish Government 2015), which is recognised as one of the most significant spore-producing hosts in the UK and has a major role in dispersal of the pathogen (Forestry Commission 2017; Scottish Government 2015). Recently, it has been shown that sporulation levels on larch (*Larix* spp.) greatly surpass that on other foliar hosts, such as *Rhododendron ponticum*, *Castanea sativa* and *Vaccinium myrtillus* (Harris and Webber 2016). The pathogen was confirmed on Japanese Larch (*Larix kaempferi*) in Cornwall (Brasier and Webber 2010) and on a Sitka Spruce (*Picea sitchensis*), economically the most important conifer grown in Britain, growing amongst *L. kaempferi* in the south of Ireland (Forestry Commission 2017). These outbreaks were followed by others in Japanese Larch plantations across Britain (Forestry Commission 2017).

48 *Phytophthora ramorum* is well adapted to cool temperatures, with sporulation occurring in periods
49 of high rainfall, humidity and mild weather (Grünwald et al. 2012). In laboratory conditions, isolates
50 showed growth when incubated between 2–28 °C (optimal temperature 16–26 °C), with
51 chlamydospores produced between 8–28 °C (optimal production at 14–26 °C) and sporangia at 6–26
52 °C (optimal production at temperature ranging 16–22 °C) (Englander et al. 2006). The suggested
53 modes of dispersal include rain and wind, rivers and streams, human activities and animals.
54 Zoospores are released in moist and cool conditions (Davidson et al. 2002; Sansford and Woodhall
55 2007) and, whilst not thought to be dispersed by wind alone, may be carried in rainwater splash
56 from foliage of an infected host to nearby plants, or in rain and mist driven by the wind (Davidson et
57 al. 2005; Davidson et al. 2002; Turner et al. 2006). Human activities affect spread of the pathogen
58 through movement of plants in the nursery trade (Goss et al. 2009; Sansford and Woodhall 2007).
59 Animals have been suggested as possible vectors for *P. ramorum*, mainly due to the patchy nature of
60 the outbreaks. There is no evidence that insects are involved in the spread of *P. ramorum* (e.g. Defra
61 2005; Kliejunas 2007) but gastropods have been identified as potential vectors, as chlamydospores
62 ingested by slugs, such as *Arion vulgaris* and *Derocerus reticulatum*, remain viable when excreted
63 (Parke et al. 2008; Telfer et al. 2015). Birds are potentially more suitable candidates as long-distance
64 vectors of *P. ramorum* than invertebrates as they tend to move further. Comparison of maps, of
65 migration routes (Wernham et al. 2002) and the main concentrations of *P.* ramorum occurrence in
66 Britain (Defra 2009), suggests some correlation between the migration routes of certain bird species,
67 such as Blackbird and Song Thrush, and the main concentrations of *P. ramorum* occurrence in Britain
68 (Defra 2009), although it is not clear if this apparent association is causal.

69 Three mechanisms of avian vectoring have been suggested. Firstly, birds may carry sporangia on
70 their feathers after being in contact with infested rainwater (Davidson et al. 2002). The second
71 possible mechanism is via soil/debris containing inoculum being carried on the feet of birds. Spores
72 of *P. ramorum* can be picked up from the soil by vehicles and other human activities and remain
73 viable (*e.g.* Cushman and Meentemeyer 2008; Davidson et al. 2005; Webber and Rose 2007). There

is therefore the potential for any ground-foraging species of bird with some association with sites containing *P. ramorum* infected plants to pick up spores of the pathogen on their feet whilst walking over/foraging through soil containing inoculum, which could then potentially be transported to new areas. The third mechanism is via ingestion of spores and excretion in the faeces. Whilst the viability of *P. ramorum* spores excreted by birds has not been tested, to our knowledge, it cannot be excluded that spores remain viable after passing through the digestive system of birds, as they remain viable when excreted by invertebrates (Parke et al. 2008; Telfer et al. 2015).

This study investigated the possibility of birds acting as vectors of *P. ramorum* within Britain by establishing if they carried spores and if so, what bird species were involved and when spores might be found. Establishing the presence of spores on birds is a prerequisite to more detailed studies of the number and level of viability of pathogen propagules found on birds and the potential for movement and subsequent infection.

2 | MATERIALS AND METHODS

2.1 | Selection of bird species

Migratory bird species which associate with, or which are likely to come into contact with, the main sporangia-producing host plant species Japanese Larch (*Larix kaempferi*) and/or *Rhododendron* spp. (Brasier and Webber 2010; Davidson et al. 2002) and which are, therefore, most likely to pick up *P. ramorum* inoculum were considered. The list was refined by selecting those species likely to be caught in high numbers, to achieve a suitable sample size, and that may come into contact with spores of the pathogen. In particular, species were selected among those that may pick up spores that have been washed off the host plants onto the ground during high rainfall in late winter/early spring (identified as the time with most widespread *P. ramorum* sporulation, mainly on infected *Rhododendron* spp. [Turner et al. 2006]) and during the spring and autumn peak sporulation periods

on larch (Dougan 2013), in Britain. These were migratory winter thrushes: Redwing (*Turdus iliacus*), Fieldfare (*Turdus pilaris*) and migratory Blackbird (*Turdus merula*) from Scandinavia (identified by plumage and measurements). Finally, we also chose species that migrate or disperse along a route which completely or partially follows the west coast of Britain during late winter/early spring. These summer migrants were: Chiffchaff (*Phylloscopus collybita*), Willow Warbler (*Phylloscopus trochilus*), Garden Warbler (*Sylvia borin*) and Blackcap (*Sylvia atricapilla*). For the purpose of this study, Winter was defined as December-February, Spring as March-May, Summer as June-August and Autumn as September-November.

2.2 | Sampling

Sampling took place between April 2011 and March 2012 at sites located along the west side of Britain, in or nearby areas associated with presence of *P. ramorum* (Figure 1). Qualified volunteer ringers caught birds using mist-nets as part of their normal ringing operations, with sessions occurring once a week, weather permitting. Each bird was placed in a cloth bag used to hold them temporarily before sampling and measuring the birds. Each bag was used only once for each bird sampled before being washed at 90° C and dried to kill any spores prior to reuse. Each individual was ringed with a uniquely identifiable metal ring and measured following standard methodology (Redfern and Clark 2011). Two swabs, each with a moist tip (BD Sterile swabs with sterile isotonic solution; Fisher Scientific, UK) were taken from each individual: one on the flank of the bird (as an identifiable and repeatable area to sample), identified as the area below the closed wing but above the thigh, the other from the toes of one of the bird's tarsometatarsi (the "foot"). No faecal samples were collected as obtaining faces from each bird would have been inconsistent, so this potential 'substrate' was not examined. The flank was chosen because: a) it would be exposed to any spores as the bird moved within the foliage whether the wing was open or closed, and b) the area was easily identified and therefore consistent sampling could be achieved within and between ringers. The toes were chosen because they would be exposed to spores on the ground as well as on

branches. The ringer taking the swab wore disposable nitrile gloves, which were either changed or wiped clean with wet wipes and air-dried before handling the following bird, to avoid cross-contamination. Ringers were asked to rotate the swab on the toes to ensure all the tip would come into contact with possible spores. The same methodology was applied to swab the flank. They were also warned that the tip of the swab should not touch any other surface before or after the sample was taken to avoid contamination. Each swab was placed in a sterile tube containing Swab Rinse Kit solution to prevent desiccation, and labelled. After sampling, tubes with the swab tip were stored between 1 and 20 °C to preserve the viability of the spores, and despatched to the laboratory by the following day via first-class post. Swabs were analysed at the University of Aberdeen (see below) on the day after receipt.

2.3 | Laboratory analyses

2.3.1 | Isolation of *P. ramorum*

Swabs were gently rubbed on the surface of PARPH V8 agar (Jeffers 2006), containing 50 ml clarified V8 juice, 950 ml d H_2O and supplemented with: 5 mg L^{-1} pimaricin, 250 mg L^{-1} ampicillin sodium salt, 10 mg L^{-1} rifampicin, 50 mg L^{-1} PCNB, and 50 mg L^{-1} hymexazol. Petri dishes were incubated at 20°C for 10 days and checked for *Phytophthora*-like growth at 48 hour intervals.

2.3.2 | Nested PCR

DNA was extracted using QuickExtract™ kits (Cambio Ltd.). Each swab was washed in 500 µl of QuickExtract™ solution which was subsequently mixed and placed in a water bath at 65°C for 30 minutes, vortexed and replaced in a water bath for a further 15 minutes at 98°C. DNA extracts were stored at -20°C until further use. DNA extracted from a pure culture of *P. ramorum* was used as a positive control in PCR reactions; ultra-pure water was used as a negative control. The nested PCR reaction was based on the protocol of Hayden et al. (2004), and involved two rounds of amplification with two primer pairs specific to *P. ramorum*. The first primer pair was:

Phyto 1: 5’-CAT GGC GAG CGC TTG A-3 and Phyto 4: 5’-GAA GCC GCC AAC ACA AG-3’

and the second primer pair, designed internal to the first pair, was:

Phyto2: 5’-AAA GCC AAG CCC TGC AC-3’ and Phyto3: 5’-GGT GGA TGG GGA CGT G- 3’

For the first amplification, 2 µl template DNA was mixed with 18 µl Mastermix (5x colourless GoTaq® reaction buffer [Promega, Madison, USA]; 0.2 µM primers Phyto 1 and Phyto 4 [Sigma Aldrich, UK]; 0.2 µM dNTPs [Promega, Madison, USA], 1 unit GoTaq® DNA Polymerase [Promega, Madison, USA]. Amplification was carried out in a Techne TC-412 thermal cycler under the following conditions: initial denature at 95°C for 3 minutes; 30 cycles at 94°C for 30 seconds, 55°C for 30 seconds and extensıon at 72°C for 1 minute. Final extension was for 10 minutes at 72°C.

The PCR products from the first amplification were diluted 1/500 in ultra-pure water, and 2 µl used as the template DNA for the second amplification. The mastermix for this second PCR included the same reagents listed above, but with 0.2 µM each of primers Phyto 2 and Phyto 3 [Sigma Aldrich, UK]. Amplification was carrıed out using the same conditions as for the first PCR. PCR products were loaded onto 1% TAE agarose gels stained with SYBR® and visualised in a UVIdoc HD2 standalone gel documentation station (Uvitec Cambridge).

2.4 | Statistical analysis

We calculated prevalence of infection and its confidence interval following binomial probability (Venables and Ripley 2002). All data analyses were undertaken using R 3.5.3 (R Core Development Team 2019).

3 | RESULTS

Over a 12-month period, twelve ringing groups/individuals caught birds at 34 sites (Table 1, Figure 1) collecting 2,017 samples from 1,014 individuals (Table 2). As Song Thrush (*Turdus philomelos*) occurred in mixed flocks with the target species, it was also sampled. The most numerous species caught among the migratory winter thrushes was Redwing, followed by Fieldfare, while among the summer migrants the most numerous was Willow Warbler, followed by Blackcap and Chiffchaff (Table 2).

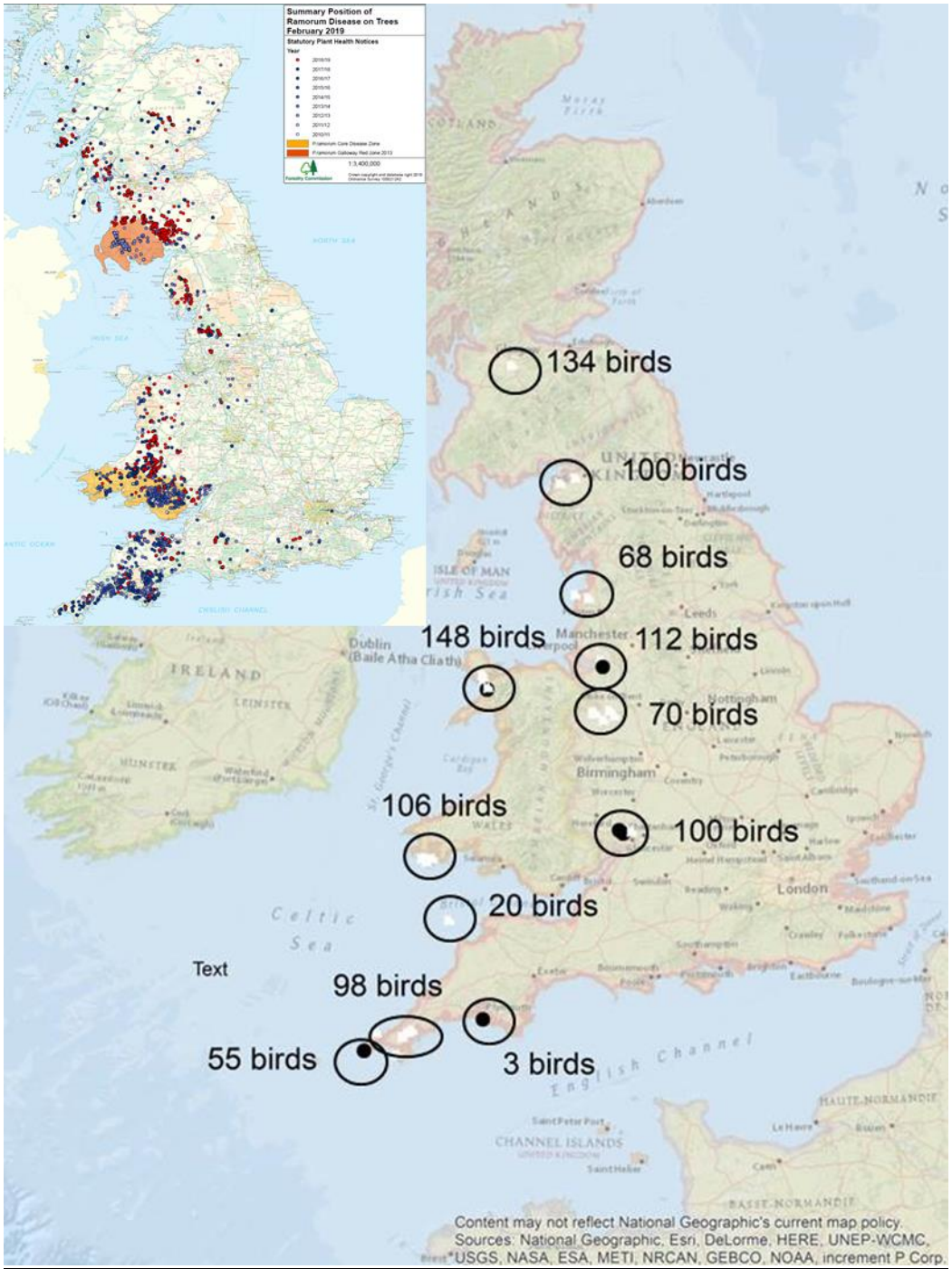
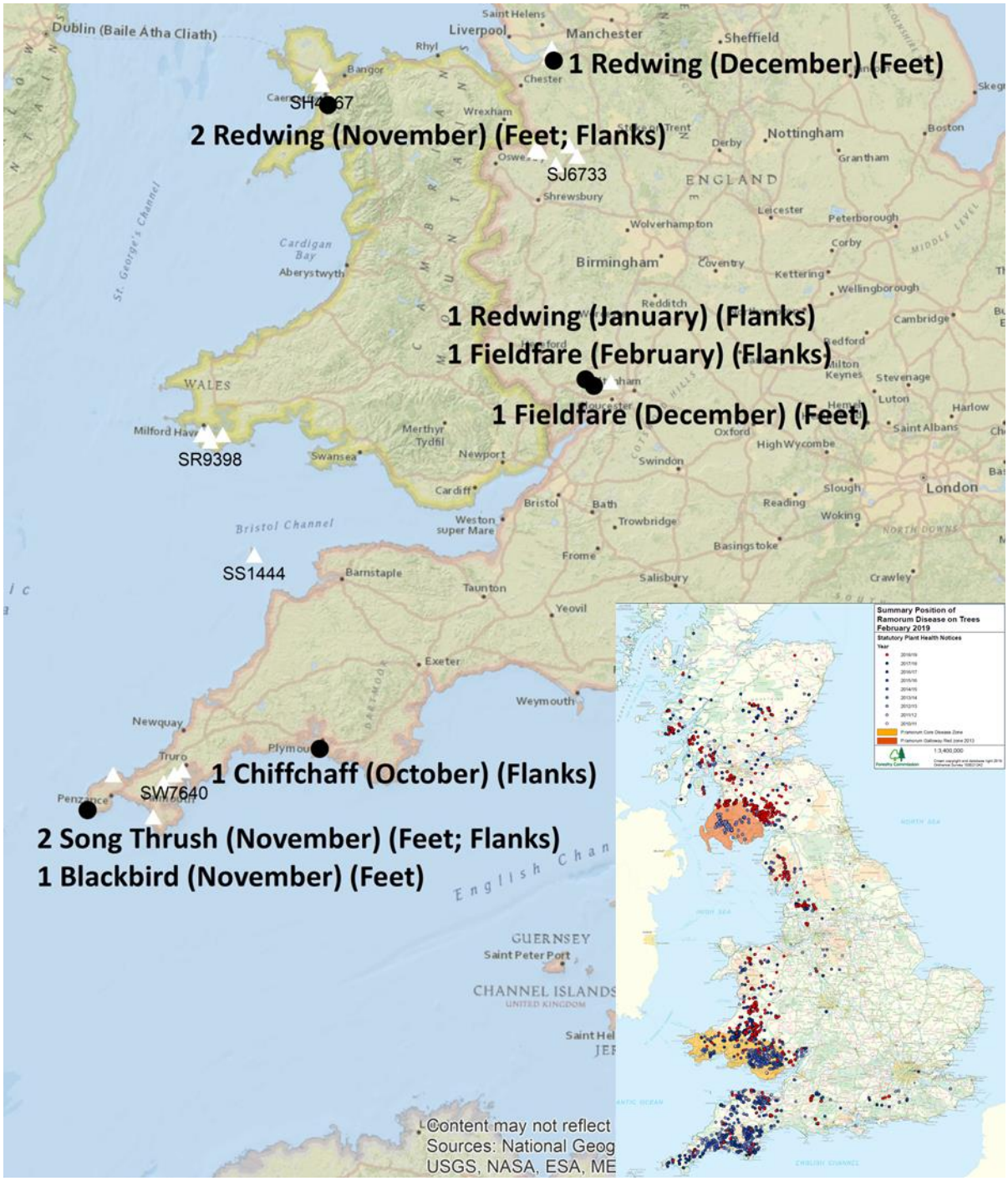


FIGURE 1 Distribution of sites at which sampling took place, with number of birds caught at each site. The black triangles show sites where all swabs were negative, red dots are sites where at least one swab from one bird tested positive. Locations of *P. ramorum* outbreaks on trees in Britain is shown in the insert (Crown Copyright, courtesy Forestry Commission (2013), licensed under the Open Government and available at www.forestresearch.gov.uk/tools-and-resources/pest-and-disease-resources/ramorum-disease-phytophthora-ramorum/). In insert map: dark blue dots are natural environment sites positive for *P. ramorum* to 1 July 2012, purple dots are positive *P. ramorum* on larch to 26 June 2012 and green dots are sites that tested negative to *P. ramorum* to 10 April 2012 (Forestry Commission 2013).

3.1 | Detection of *Phytophthora ramorum*

The culturing method was initially used on 600 swab samples but no *Phytophthora* species were detected; numerous hyphal and yeast-like true fungi were found, but were not identified further. The same 600 samples, plus the remaining 1,417 swabs which were not cultured, were analysed directly using nested PCR.

Phytophthora ramorum was detected using PCR tests in ten samples equating to an overall average prevalence rate of 1%. Prevalence ranged between 2% and 100%, varying between bird species, site and month (Table A1). Confidence intervals (CIs) around each prevalence varied greatly, the lower ones ranging from 0.005 – 2%, and the upper CIs between 11 – 100% (Table A1). Five positive swabs were from feet and five from flanks. All birds that were positive for presence of *P. ramorum* were caught in autumn/winter 2011/2012 - one in October, five in November, two in December, one in January and one in February (Table A1). The positive samples were from four Redwings, two Song Thrushes, one Blackbird, two Fieldfares and one Chiffchaff coming from six sites (Figure 2).



200

201 **FIGURE 2** Distribution, species, number, month and provenance of positive sample (feet or flanks) of
202 birds positive for presence of *P. ramorum* using nested PCR. Black triangles are sites where no swabs
203 were positive, red dots are sites where at least one swab from one bird tested positive. Locations of
204 *P. ramorum* outbreaks on trees in Britain is shown in the insert (Crown Copyright, courtesy Forestry
205 Commission (2019), licensed under the Open Government and available at
206 www.forestresearch.gov.uk/tools-and-resources/pest-and-disease-resources/ramorum-disease-

phytophthora-ramorum/). In insert map: dark blue dots are natural environment sites positive for *P. ramorum* to 1 July 2012, purple dots are positive *P. ramorum* on larch to 26 June 2012 and green dots are sites that tested negative to *P. ramorum* to 10 April 2012 (Forestry Commission 2013).

4 | DISCUSSION

In this study we have shown that some passerine species, especially ground-foraging ones, can be contaminated with *P. ramorum* in autumn and winter, albeit at low frequency. All individual birds that tested positive for the presence of *P. ramorum* were sampled in the autumn/winter months, in or near forests known to be affected by the pathogen and close to the coast. The number of birds sampled was higher in spring/summer 2011 (Table 2) when no positives were found. However, precipitation during spring (April and May 2011) was below average (Royal Meteorological Society 2011a), which would have affected sporulation negatively, therefore in a wetter year we cannot exclude that some positives would have been found. Rainfall was average for the summer months (June to August 2011) (Royal Meteorological Society 2011b), suggesting that the results for these months may be typical of an average rainfall year.

The culturing method was deemed not sensitive enough for the low presence of spores in each swab and molecular analyses in the form of nested PCR were utilised. The low incidence of positive samples, even when testing with the hıghly sensitive nested PCR method suggested that either spores of *P. ramorum* were not present on the birds at high frequency, or that, although unlikely, birds may have lost spores prior to sampling. The number of individuals which tested positive in a site never exceeded two, regardless of the number of birds sampled (Table A1). This finding suggests that, over the period that sampling took place, the frequency of birds carrying spores was low, although the probability of carrying inoculum could potentially be higher in some months and for some species (see CIs in Table A1). It is likely spores are picked up by chance, rather than being a predictable occurrence, even where the incidence of *P. ramorum* might be expected to be high. In

addition, most positive samples were collected from ground-feeding birds which are more likely to have spores adhering to the feet, but only five samples taken from feet tested positive for *P. ramorum*. In an experiment, Turner et al. (2006) found that *P. ramorum* can survive in the soil on artificially-infested leaves for two winters in the UK. This suggests that the soil can be an important source of spores, which ground-foraging birds can pick up. Thrushes dislodge the ground leaf litter to look for invertebrates (Brown and Grice 2005), and in doing so may come into contact with infested raindrops. These birds, therefore, may be more likely to collect spores than birds that live almost exclusively in the canopy.

Of the four species of thrush which were found to be carrying spores, two (Fieldfare and Redwing) are migrants. The main influx of Fieldfare into Britain occurs in October and November (BTO/RSPB/BirdWatch Ireland/SOC/WOS Birdtrack, 2019). By December, very few movements are long-distance (over 100 km) and Fieldfare are mostly settled on their wintering grounds making only local (up to 10 km) movements until migration to breeding areas in Fennoscandia the following spring (Milwright 1994; Wernham et al. 2002). As the positive results from Fieldfares were of birds sampled in December and early February, the individuals would not be migrating, and hence were unlikely to have acted as long-distance vectors of *P. ramorum*.

The influx of Redwing in October and November (BTO/RSPB/BirdWatch Ireland/SOC/WOS Birdtrack, 2019) involves long-distance migration, but by December birds have settled into the wintering areas (Milwright 2002) and movements are mainly associated with food source availability (Wernham et al. 2002). The colder months (December, January and often February) may be characterised by shorter, local, movements in many migrant Redwings overwintering in Britain. The Redwings caught in November that tested positive may have moved on as part of their usual migratory route, and any such movement would have been towards France or the Iberian Peninsula, passing through Cornwall

(Wernham et al. 2002). The other two individuals that tested positive were sampled in December and January, and it is unlikely that they would have moved far from the site of ringing until spring.

Two Song Thrushes, caught over a two-week period in mid-November, also tested positive for the pathogen. These birds were from the same site in Cornwall, which has Japanese Larch plantations damaged by *P. ramorum* (www.forestry.gov.uk/pdf/PramorumOutbreakMapJuly2017.pdf). Although Song Thrush is mostly sedentary in Britain & Ireland (Wernham et al. 2002), the species tends to mix with the target species when it is possible that spores could be transferred between birds either by direct contact or by contamination of common ground soil. Song Thrush also uses a broad range of habitats which include deciduous woodland and conifer plantations – from open ground to bushes or trees (Brown and Grice 2005), making this species a candidate to collect spores from the environment and potentially pass them to the other species. However, the three birds were caught within a two week period in the middle of November (Table 3) and it is unlikely that they could have passed any spores to migratory species, such as Redwing and Fieldfare, which have the potential to spread propagules throughout Britain at that time of year. Redwings in that area would have been settled for winter, or may have been on migration to France and the Iberian Peninsula (Milwright 2002; Wernham et al. 2002). Fieldfare present in the area would move only locally throughout the winter, although some individuals may have been using the site as staging area to migrate to the south of Europe (Wernham et al. 2002). However, no Fieldfare or Redwing was positive for *P. ramorum* from the same site or sites nearby.

A Blackbird caught in Cornwall in November also tested positive. The British wintering population of Blackbird comprises both local breeders which are sedentary and migratory birds, with the latter apparently more predominant in the north of Britain and the southeast (Wernham et al. 2002). There are very few reports of movement of Blackbirds ringed ın the west of Britain, including movements within Britain and between eastern Europe and southwest England (Robinson et al.

2018). At the time the individual that tested positive was sampled (November), migratory Blackbirds would only be moving locally until spring migration back to the breeding ground.

Summer migrants (species found breeding in Britain but which overwinter elsewhere) did not test positive for *P. ramorum*, despite the higher sample size, suggesting that the amount of inoculum on the birds considered was very low or absent, although formal quantification using molecular tools was not within the scope of this project. One Chiffchaff in Devon tested positive in October, from an area where the species is known to overwinter in increasing numbers over recent years (Conway 2011; Wernham et al. 2002). It is uncertain whether this bird was departing on autumn migration or overwintering in Britain, but in either scenario the individual would not have moved to the north of Britain until the following breeding season, as wintering birds remain mainly in the south (Wernham et al. 2002), only moving locally until spring migration. A small number of individuals of this species ringed in southwest Britain, including Devon, have however been recovered as far north as Scotland during the same spring (Robinson and Clark 2012).

Birds caught and sampled in this study are believed to be a true representation of the general population present in areas affected by *P. ramorum*, as no biases were introduced in targeting individuals that were likely infected or not infected. This study assumed that all birds sampled had the same chance to encounter spores, but this may not be the case. For example, ground-foraging birds such as thrushes may have a higher chance to encounter spores than leaf-dwelling warblers, although this was not tested. The incidence of spores found on birds was low. This was unlikely due to sampling methodology, as, for example, spores dislodged from the bird whilst in the bird bag would have likely been spread all over the plumage, including the target sampling areas, as the individual moved in the bird bag. We do recognise that the probability of a bird carrying spores could have been higher than those reported here, simply due to chance (Table 2). Nevertheless, the numbers of birds involved compared to the number of total individuals sampled would have remained low, albeit potentially contributing to local spread (see later).

Weather is an important factor to consider when putting our results into context. Precipitation levels in winter 2011/12 (December 2011 to February 2012) had been variable throughout the sampling areas but lower than or on average in areas were positive bird samples had been detected (Royal Meteorological Society 2012), presumably leading to drier-than-average soil and sporulation of *P. ramorum*. A similar pattern may have applied for spring 2011, when precipitations had been low compared to average (Royal Meteorological Society 2011a), which in turn would have not been conducive to *P. ramorum* sporulation, a factor that should be considered when interpreting the negative results; more typical rainfall levels might have led to more positive samples but further work would be needed to test this hypothesis. Conversely, rainfall in summer 2011 had been average (Royal Meteorological Society 2011b), conditions that should translate to a typical amount of spores in the environment but no positive samples had been recovered, suggesting either that presence of spores was low, or that birds did not pick them up in high enough frequency to be detected in this study, or that passerine birds are not frequent vectors. This result may also be due to the different behaviour of winter-sampled birds, which fed on the ground and hence were potentially more likely to pick up spores than summer-sampled species which were leaf dwellers. Summer species were not necessarily associated with larch, where they might have had higher probabilities to come into contact with *P. ramorum* than on other plants. However, the sites selected had *Rhododendron spp.*, a host plant associated with *P. ramorum* sporulation albeit at lower levels than larch (Harris and Webber 2016).

In this study we have shown that some passerine species, especially ground-foraging ones, can be contaminated with *P. ramorum*. Waterbirds and species associated with waterways, such as Yellow Wagtail (*Motacilla flava* spp.) and Dipper (*Cinclus* cinclus), were not tested because of sample size restrictions, but given the persistence of *P. ramorum* in waterways and their role in spreading of spores (e.g. Peterson et al. 2014; Reeser et al. 2011; Sutton et al. 2009; Davidson et al. 2005), further studies should consider those species, too.

Prevalence was low for all species sampled and across the year. Results from an epidemiology study of *P. ramorum* in Oregon, USA, showed that the frequency of new infection in Oregon tanoak (*Notholithocarpus densiflorus*) forests was highest within 300 m of infected trees, but it decreased rapidly over 1 km away(Hansen et al. 2008), although new infections can be detected as far as 5.5 km away when transported by waterways, albeit following a seasonal pattern of less likelihood of detection in colder months (Sutton et al. 2009). Local spread, therefore, may occur frequently, with longer-distance spread being less frequent. In the current study a Redwing which might have been heading south towards France or the Iberian Peninsula tested positive, therefore the individual could have acted as vector of infected spores. We can also not exclude that migratory birds in general can carry inoculum whilst on migration. However, these hypotheses should be investigated with further work, as the viability of spores carried by birds and other animals has not been investigated. The apparently stochastic pattern observed in this study could possibly match the movements of birds, with high-frequency local spread facilitated outside the migratory period by both migratory species and sedentary species alike, and spores subsequently spread less frequently over long distances by either birds or other means, such as wind (Hansen et al. 2008). This scenario would match the high-frequency local distance and low-frequency of long-distance cases found by Hansen et al. (2008). Other animals have also been implicated as vectors of *Phytophthora* spp.. Previous studies have found that non-avian taxa could be associated with new outbreaks of *Phytophthora spp.*; these included goats (*Capra aegagrus hircus*) (Cardillo et al. 2018), feral pigs (*Sus scrofa*) (Li et al. 2014) and slugs (Telfer et al. 2015; Parke et al. 2008), the latter two showing viable spores excreted after ingestion of infected material. The role of animals in the spread of *P. ramorum* is still unclear and under-studied. Further research should focus on whether inoculum on birds remains viable, and whether it can be transported to new plant hosts. An experimental approach would be ideal but replicating natural conditions with wild birds in a laboratory setting would be challenging. Other possible vectors in Britain should also be considered, including mammals that use potentially infected habitats, such as Grey Squirrels (*Sciurus carolinensis*) and deer (Cervidae). Other bird

356 species more closely associated with larch (e.g. Siskins *Spinus spinus*, Bramblings *Fringilla*
357 *montifringilla*) could also be investigated, if a big enough sample size could be achieved, and may
358 lead to higher incidence of positive samples. The spread of *P. ramorum* in Britain is likely due to a
359 number of vectors, biotic and abiotic, perhaps working synergistically. A modelling approach should
360 be applied to investigate this possibility. The present study suggests that, at least under the weather
361 conditions encountered during this study, *P. ramorum* can be found on passerine birds at low
362 prevalence, both during a dry spring as well as a wet summer when conditions for sporulation were
363 likely optimal. All detections occurred on ground-feeding birds during autumn and winter, which
364 were characterised by low precipitation, suggesting that contamination of birds can occur at
365 presumably low inoculum production, or that inoculum was still present in the soil from previous
366 years, as it has been shown to occur (Turner et al. 2006). The migration patterns of the bird species
367 that had tested positive for spores does not support the hypothesis of a direct spread of the disease
368 northwards, although it cannot be excluded that some individuals may have carried inoculum when
369 moving southwards. The results obtained in this work suggest that passerine birds can carry *P.*
370 *ramorum* inoculum on their feathers and "feet", albeit at low frequency. Further work is needed to
371 estimate the extent of their contribution to the spread of *P. ramorum* in Britain.

372

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384

385

386 **TABLE 1** Sites and number of birds sampled over the 12 month period (2011-2012).

Site Grid Reference	**Site Name**	**County**	**Number of birds**
NS7257	Strathclyde Loch	North Lanarkshire	134
NY1748	Crooklands	Cumbria	8
NY3153	Great Orton	Cumbria	92
SD3145	Fleetwood	Lancashire	11
SD4342	Rawcliffe Moss	Lancashire	57
SH4571	Glan - Morfa	Isle of Anglesey	59
SH4667	Bodrida	Isle of Anglesey	13
SH4957	Rhostryfan	Gwynedd	53
SH5059	Tyddyn Gwydd	Gwynedd	23
SJ4736	Oaf's Orchard	Wrexham	14
SJ4935	Whixall Moss	Shropshire	20
SJ4936	Fenn's Moss	Shropshire	10
SJ5480	Palace Fields, Runcorn	Halton	1
SJ5583	Manor Park, Holton	Halton	10

SJ5584	Manor Park, Holton	Halton	97
SJ5678	Aston	Cheshire	4
SJ5729	Hawkstone Park	Shropshire	3
SJ6338	Shavington Park	Shropshire	18
SJ6733	Market Drayton	Shropshire	5
SM8901	Kilpaison Burrows	Pembrokeshire	47
SM9202	Pwllcrochan	Pembrokeshire	28
SM9901	Pembroke	Pembrokeshire	13
SO7127	Three Ashes	Gloucestershire	93
SO7524	Rymes Place Farm	Gloucestershire	7
SO8326	Hasfield	Gloucestershire	0
SR9398	Axton Hill	Pembrokeshire	18
SS1444	Lundy Island	Devon	20
SW3523	Nanjizal	Cornwall	55
SW4740	Treveal	Cornwall	63
SW6620	Winnianton Farm	Cornwall	3
SW7136	Stithians Reservoir	Cornwall	1
SW7640	Cusgarne	Cornwall	10
SW8042	Kea	Cornwall	21
SX4552	Mount Edgecumbe Country Park	Cornwall	3

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388

389 **TABLE 2** Number of birds sampled per each month across all sites. Prevalence (%) of infection and its
390 confidence interval, following binomial probability, are reported in brackets for positive samples
391 only.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Blackbird	0	0	0	0	0	0	0	0	0	24	22 (4.5 CI: 0.1-23%)	0	46
Song Thrush	0	0	0	0	0	0	0	0	0	25	12 (16.7 CI: 2-48%)	0	37
Fieldfare	8	48 (2.1 CI: 0.1-21%)	0	0	0	0	0	0	0	4	14	8 (12.5 CI: 0.3-53%)	82
Redwing	24 (4.2 CI: 0.1-21%)	12	1	1	1	0	0	0	0	31	70 (2.8 CI: 0.3-9.9%)	14 (7.1 CI: 0.1-34%)	154
Blackcap	0	0	0	18	13	50	72	37	15	13	0	0	218
Garden Warbler	0	0	0	2	13	16	11	3	0	0	0	0	45
Chiffchaff	0	0	0	15	9	21	55	76	18	6 (16.5 CI: 0.4-	0	0	200

										64%)			
Willow Warbler	0	0	0	33	32	72	70	24	1	0	0	0	232
Total	32	60	1	69	68	159	208	140	34	103	118	22	**1,014**

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APPENDIX 1

Table A1. Number of birds samples by month, site and species (2011-2012). . Prevalence (%) of infection and its confidence interval, following binomial probability, are reported in brackets for positive samples only.

Month	Site	Species	Number	Month	Site	Species	Number	Month	Site	Species	Number
January	SD4342	Redwing	3	June	NY1748	Garden Warbler	1	August	SM8901	Willow Warbler	3
January	SH4957	Redwing	2	June	NY1748	Willow Warbler	3	August	SM9202	Blackcap	13
January	SO7127	Fieldfare	8	June	NY3153	Blackcap	9	August	SM9202	Chiffchaff	15
January	SO7127	Redwing	19 (5% CI: 0.1-26%)	June	NY3153	Chiffchaff	6	August	SM9901	Chiffchaff	13
February	SJ5583	Redwing	4	June	NY3153	Garden Warbler	5	August	SW6620	Chiffchaff	3
February	SJ5678	Redwing	1	June	NY3153	Whitethroat	2	August	SW7136	Chiffchaff	1
February	SO7127	Fieldfare	48 (2% CI: 0.005-11%)	June	NY3153	Willow Warbler	26	August	SW7640	Chiffchaff	1
February	SO7127	Redwing	7	June	SH4571	Garden Warbler	1	September	SW4740	Blackcap	15
March	SJ5678	Redwing	1	June	SH4571	Willow Warbler	6	September	SW4740	Chiffchaff	18
April	SH5059	Blackcap	3	June	SH4667	Blackcap	6	September	SW4740	Willow Warbler	1
April	SH5059	Chiffchaff	3	June	SH4667	Chiffchaff	1	October	NS7257	Redwing	1
April	SH5059	Willow Warbler	6	June	SH4667	Willow Warbler	6	October	SD3145	Redwing	1
April	SJ4736	Chiffchaff	3	June	SH5059	Blackcap	2	October	SD3145	Songthrush	3
April	SJ4736	Willow Warbler	11	June	SH5059	Garden Warbler	3	October	SD4342	Blackbird	6
April	SJ4935	Blackcap	2	June	SH5059	Willow Warbler	6	October	SD4342	Fieldfare	3
April	SJ4935	Willow Warbler	8	June	SJ5584	Blackcap	3	October	SD4342	Redwing	12
April	SJ4936	Blackcap	2	June	SJ5584	Chiffchaff	3	October	SD4342	Songthrush	7
April	SJ4936	Chiffchaff	1	June	SJ5584	Garden Warbler	1	October	SH4957	Redwing	3

April	SJ4936	Garden Warbler	2	June	SJ5584	Willow Warbler	1	October	SJ5583	Redwing	1
April	SJ4936	Willow Warbler	5	June	SW8042	Blackcap	2	October	SO8326	Songthrush	1
April	SJ5678	Redwing	1	June	SW8042	Chiffchaff	1	October	SS1444	Blackbird	6
April	SJ5729	Blackcap	1	July	NS7257	Blackcap	13	October	SS1444	Fieldfare	1
April	SJ5729	Chiffchaff	2	July	NS7257	Chiffchaff	12	October	SS1444	Redwing	10
April	SJ6338	Blackcap	1	July	NS7257	Garden Warbler	6	October	SS1444	Songthrush	3
April	SJ6338	Chiffchaff	2	July	NS7257	Willow Warbler	23	October	SW3523	Blackbird	12
April	SJ6733	Blackcap	2	July	NY3153	Blackcap	14	October	SW3523	Redwing	3
April	SJ6733	Chiffchaff	1	July	NY3153	Chiffchaff	6	October	SW3523	Songthrush	11
April	SJ6733	Willow Warbler	2	July	NY3153	Garden Warbler	2	October	SW4740	Blackcap	9
April	SW8042	Blackcap	7	July	NY3153	Willow Warbler	9	October	SW4740	Chiffchaff	5
April	SW8042	Chiffchaff	3	July	SJ5584	Blackcap	37	October	SW7640	Blackcap	2
April	SW8042	Willow Warbler	1	July	SJ5584	Chiffchaff	16	October	SX4552	Blackcap	2
May	NS7257	Blackcap	5	July	SJ5584	Garden Warbler	3	October	SX4552	Chiffchaff	1 (100% CI: 2.5-100%)
May	NS7257	Garden Warbler	7	July	SJ5584	Willow Warbler	26	November	NS7257	Redwing	1
May	NS7257	Willow Warbler	6	July	SR9398	Blackcap	2	November	SD3145	Blackbird	3
May	NY3153	Chiffchaff	1	July	SR9398	Chiffchaff	6	November	SD3145	Redwing	1
May	NY3153	Garden Warbler	1	July	SR9398	Willow Warbler	9	November	SD3145	Songthrush	2
May	NY3153	Willow Warbler	5	July	SW4740	Blackcap	5	November	SD4342	Blackbird	4
May	SH4571	Chiffchaff	1	July	SW4740	Chiffchaff	8	November	SD4342	Fieldfare	8
May	SH4571	Garden Warbler	1	July	SW4740	Willow Warbler	3	November	SD4342	Redwing	13
May	SH4571	Willow Warbler	17	July	SW7640	Blackcap	1	November	SD4342	Songthrush	1
May	SJ4935	Blackcap	2	July	SW7640	Chiffchaff	5	November	SH4957	Redwing	43 (5% CI: 0.6-16%)
May	SJ4935	Chiffchaff	2	July	SW7640	Willow Warbler	1	November	SJ5480	Blackbird	1
May	SJ4935	Garden Warbler	3	July	SW8042	Blackcap	1	November	SJ5583	Redwing	2
May	SJ4935	Willow Warbler	3	July	SW8042	Chiffchaff	3	November	SM8901	Fieldfare	1
May	SJ5678	Redwing	1	August	NY3153	Blackcap	2	November	SM8901	Redwing	4

May	SJ6338	Blackcap	4	August	NY3153	Willow Warbler	5	November	SO7127	Fieldfare	5
May	SJ6338	Chiffchaff	4	August	SH4571	Blackcap	6	November	SW3523	Blackbird	14 (7% CI 0.2-34%)
May	SJ6338	Garden Warbler	1	August	SH4571	Chiffchaff	13	November	SW3523	Redwing	6
May	SR9398	Willow Warbler	1	August	SH4571	Willow Warbler	14	November	SW3523	Songthrush	9 (22% CI: 3-60%)
May	SW8042	Blackcap	2	August	SJ5584	Blackcap	2	December	SH4957	Redwing	5
May	SW8042	Chiffchaff	1	August	SJ5584	Chiffchaff	2	December	SJ5583	Redwing	3
June	NS7257	Blackcap	26	August	SJ5584	Garden Warbler	1	December	SJ5678	Redwing	2 (50% CI:1-99%)
June	NS7257	Chiffchaff	6	August	SJ5584	Willow Warbler	2	December	SO7127	Fieldfare	3
June	NS7257	Garden Warbler	5	August	SJ6338	Chiffchaff	6	December	SO7127	Redwing	3
June	NS7257	Willow Warbler	24	August	SM8901	Blackcap	14	December	SO7524	Fieldfare	5 (20% CI: 0.5 - 72%)
June	NY1748	Chiffchaff	4					December	SO7524	Redwing	2

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