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ORIGINAL PAPER

Population crash in an invasive species following the recovery of a native predator: the case of the American grey squirrel and the European pine marten in Ireland

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Abstract In Ireland, the UK and Italy, the invasive North American grey squirrel, *Sciurus carolinensis*, threatens the survival of the Eurasian red squirrel, *Sciurus vulgaris,* as the effects of competition and disease almost inevitably lead to total replacement of red squirrel populations. However the results of a recent national squirrel survey suggested that the normally invasive grey squirrel had gone into decline in the Irish midlands, which was anecdotally attributed to an increase in European pine marten, *Martes martes*, range and numbers. This study aimed to quantify changes in squirrel distribution in Ireland and to investigate the role, if any, of the pine marten in red and grey squirrel population dynamics. A distribution survey of the midlands was carried out which confirmed the grey squirrel population has crashed in approximately 9,000 km^2 of its former range and the red squirrel is common after an absence of up to 30 years. At landscape level, pine marten and red squirrel abundance were positively correlated, whereas a strong negative correlation between pine marten and grey squirrel presence at woodland level was found to exist. Squirrel demographics were determined by means of live trapping programs which confirmed that the red squirrel in the midlands is now in competitive release and the grey squirrel is present at unusually low density. This study provides the first evidence of a regional grey squirrel population crash and suggests that European pine marten abundance may be a critical factor in the American grey squirrel's success or failure as an invasive species.

Keywords Competitive release · Grey squirrel · Hairtube survey · Invasive prey · Live squirrel trapping · Native predator · Pine marten · Population crash · Red squirrel · Sightings survey

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Introduction

There are two squirrel species found in Ireland; the native Eurasian red squirrel, *Sciurus vulgaris*, and the non-native North American grey squirrel, *Sciurus carolinensis*. In 2004 the grey squirrel was classified as one of the world's most invasive alien species due to damage caused by the bark stripping of trees in their invasive range, and the detrimental impact on red squirrel populations (Lowe et al. 2004). Indeed in Ireland, the UK and Italy the grey squirrel threatens the survival of the native red squirrel due to the effects of competition and disease. The process of competitive replacement of red by grey squirrels and its causal factors have been the subject of much research to date (e.g. Kenward and Holm 1993; Kenward et al. 1998; Wauters et al. 2000, 2002; Gurnell et al. 2004). As such there is evidence for competitive replacement of red squirrels throughout the grey squirrel's invasive range, however in Britain, squirrel pox virus (SQPV), which is carried by grey squirrels asymptomatically, but lethal to red squirrels, has also played a major contributing role in the replacement of the red squirrel (Rushton et al. 2006). Indeed with the exception of a few, small, intensively managed populations the red squirrel is now almost entirely absent from England and Wales (Rushton et al. 2006). It is not known what impact disease has had on the Irish red squirrel population historically, as the disease was not detected on the island until 2011 (McInnes et al. 2012). SQPV has not been detected in the Italian population to date.

To date, there has been no successful method developed in the long-term control (nor indeed the eradication) of grey squirrel populations. In order for control to be successful at a local level, short-term tactics must be employed intensively and on an ongoing basis (Gurnell and Pepper 1993). Lawton and Rochford (2007) found that grey squirrel control for the purpose of reducing damage to trees may be effective if carried out intensively during spring however a recovery in numbers was found to take place within 10 weeks of intensive culling programs. Worryingly, Bertolino et al. (2008) predict that if the existing grey squirrel population in Italy is not contained successfully, it will continue to spread to France and Switzerland within a matter of decades and eventually potentially to much of Eurasia.

In Ireland, the grey squirrel was introduced from its non-native range in Britain in 1911 to one known location in the midlands (Castleforbes Estate, Co. Longford). Since then, the population has spread through much of the north, east and south of the country, at a mean rate of 1.94 km per year (O'Teangana et al. 2000). The most recent survey found grey squirrels present in 26 (of 32) counties (Carey et al. 2007), with the west and southwest representing the only parts of the country in which the grey squirrel had not yet established itself. O'Teangana et al. (2000) noted for the first time however, that red and grey squirrel populations in some northern counties appeared "unsettled" and that the grey squirrel had been reported, anecdotally, to have declined locally since the 1980s, allowing for a red squirrel population resurgence. In 2007, Carey et al. found a similar phenomenon to be occurring, namely grey squirrels declining and red squirrels reappearing after an absence of several decades, in the midland counties of Laois and Offaly. This apparent retraction of the grey squirrel's range coincided with the regionally resurgent pine marten, *Martes martes*, population, and anecdotal evidence suggested the distribution patterns of the three species may be linked (Carey et al. 2007).

The pine marten has been hunted heavily for its fur throughout its range, and in Ireland predator control programs and habitat loss through deforestation, combined with hunting for fur, led to a major reduction in range by the twentieth century (O'Sullivan 1983). O'Sullivan conducted the first comprehensive national survey of pine marten in the 1980s which found the population to be largely restricted to counties west of the river Shannon, with one other small population in the Slieve Bloom mountain range in counties Laois and Offaly. A second survey in 2006 found these core populations had increased in recent decades, as a result of increased habitat availability through reforestation and importantly, protection by law under the Wildlife Act (1976) O'Mahony et al. (2006).

There is no evidence in the literature of either European or American marten species being a limiting force on tree squirrel populations (Gurnell 1987; Smith 2007). The European pine marten is a known predator of the Eurasian red squirrel, however the percentage frequency of occurrence (%FO) in the diet has been found to be very low (e.g. between 0 and 2.5 % in Ireland and Scotland) (Warner and O'Sullivan 1982; Balharry 1993; Gurnell and Lurz 1997; Lynch and McCann 2007; Caryl et al. 2012; O'Meara et al. 2013; Sheehy et al. 2013) despite the extensive overlap in ranges of the two species.

In contrast, little is known about marten predation on the North American grey squirrel. The natural range of the grey squirrel in North America only overlaps with that of the American marten, *Martes americana*, and fisher, *Martes penanti*, in a very small part of its north eastern and north western natural range limits. Where studies have been carried out in North America, the grey squirrel has appeared as a higher frequency prey item (16 and 17 % FO) in the diet of the American marten and the fisher respectively (Hales et al. 2008; Arthur et al. 1989). The range of the grey squirrel has only coincided with the range of the European pine marten in very recent years in Ireland and in Scotland. A recent study has found evidence of pine marten predation on grey squirrels in the east of Ireland at a rate similar to that of the American marten species (15.6 % FO) in their natural range (Sheehy et al. 2013). As the pine marten population has begun to recover in both countries it has been suggested anecdotally that the range of the grey squirrel has retracted (Paterson and Skipper 2008; Carey et al. 2007). However, to date there has been no quantification of the apparent range retraction of the grey squirrel in Ireland or in Scotland. If the grey squirrel population has in fact experienced a sustained decline in Ireland, as has been anecdotally suggested, it is atypical for the species anywhere in its invasive range and could prove highly significant both in terms of red squirrel conservation in Ireland, the UK and Europe and also in the reduction in damage to commercial forestry.

The aims of this study were to quantify the suggested range retraction of the invasive grey squirrel in Ireland and to investigate the role, if any, of the European pine marten in red and grey squirrel population dynamics.

Materials and methods

There are five established field methods for the indirect monitoring of squirrel populations, as described by Gurnell et al. (2001a). In the current study hairtube surveys, combined with a sightings survey which targeted professionals and drew upon citizen science, were chosen as the optimum methods for indirectly determining which species of squirrel were present across a wide area and a range of survey sites. The use of hairtraps in evaluating both presence and abundance of pine marten has been used successfully in Ireland (Lynch et al. 2006; Mullins et al. 2010; Sheehy et al. 2013) and thus was selected as the optimum method, alongside the sightings survey as above, for detecting pine marten presence across the variety of survey sites.

Three study areas were selected as follows: Laois and Offaly (referred to hereafter as the midlands study area), where a possible grey squirrel decline and red squirrel recovery had been reported by Carey et al. (2007) and a pine marten recovery had been reported by

Fig. 1 Locations of the midlands, east and buffer zone study areas in Ireland, and the 18 squirrel and pine marten hairtube survey sites (1–18). Live-trapping site Charleville forest = 3* and Tomnafinnoge = 10*

O'Mahony et al. (2006); Wicklow (referred to hereafter as the eastern study area) where all three species were recorded as present but the phenomenon of grey squirrel decline had not been reported; and the buffer zone study area (which consisted of a 30 km radius zone surrounding the midlands study area (Fig. 1).

Animal sightings were collected between January 2010 and December 2012. The survey was advertised primarily by means of colour posters placed in population centres throughout the study areas, and also local media such as newspapers and radio stations. Foresters, ecologists and wildlife rangers were targeted for their knowledge on local species' distributions. The National Association of Regional Game Councils (NARGC) supplied >900 of their member clubs with sightings survey forms, and there was also national newspaper and television coverage of the survey. Strict validation criteria were adhered to, where only those sightings that were either accompanied by photographic evidence, described as stationary (roadkill) animals, came from a professional (e.g. forester, ecologist) or had description adequate to be deemed reliable were accepted. Those that did not have sufficient contact information, location information or were in any way unclear about the species seen were rejected. All sightings were assigned a grid reference, and any sighting of the same species reported within a 1 km radius of another was considered a duplicate and therefore not included in the analysis. As such each sighting location was based on a unique 1 km^2 point location thus the possible influence of species being reported multiple times in areas or sites that are more heavily frequented by humans was reduced as far as possible.

In total, 18 sites were selected for hairtube survey (Fig. 1). In the midlands, only sites within the grey squirrel's range at landscape level (as per published data in O'Teangana et al. 2000) and where woodland owners, managers or gamekeepers could also confirm the

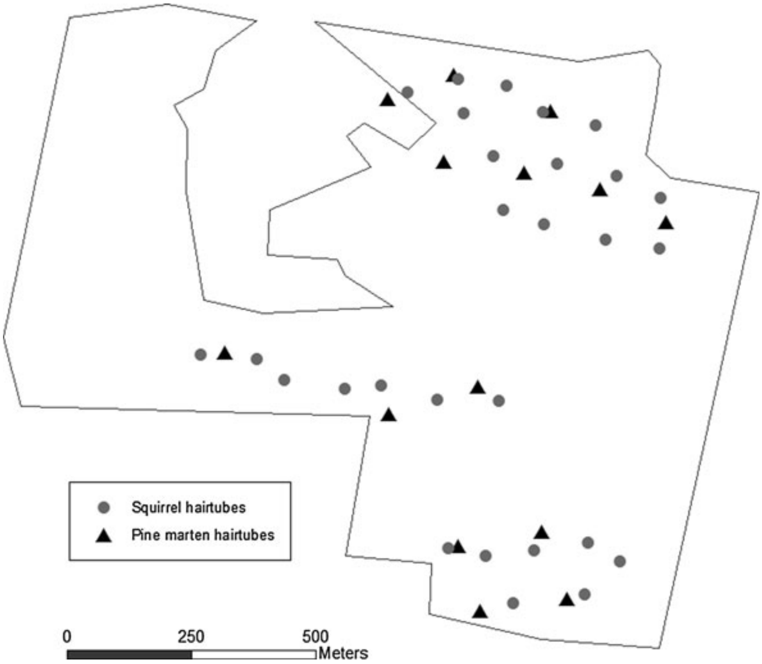


Fig. 2 Position of squirrel ($n = 28$) and pine marten ($n = 14$) hairtubes at site 3. Squirrel hairtubes were placed at a density of one per hectare and pine marten hairtubes at one per two hectares in three adjacent grids

grey squirrel had been established in large numbers at woodland level historically were selected. Between 14 and 30 squirrel hairtubes and 7 and 15 pine marten hairtubes were installed at each site for a period of 14 days. Squirrel hairtubes as described by Gurnell et al. (2001a) were installed at a density of one per hectare in a continuous grid where possible, but often in two to three smaller grids within the wood (Fig. 2). Pine marten hairtubes as described by Mullins et al. (2010), baited with chicken and marmalade were installed at a density of one per two hectares within the same grid system as the squirrel hairtubes (Fig. 2).

Hair samples were classified as either squirrel, pine marten or other mammal by means of cuticular analysis (Teerink 1991) and in order to distinguish between the two squirrel species, cross sectional analysis as per Teerink (1991) was carried out.

Arcview 9.3 was used to map the point for each unique sighting location (min 1 km radius) and a 10 km radius kernel density was then used to display patterns of distribution and abundance of sighting locations for each species. The number of unique sighting locations per species were counted for each hectad within the midlands ($n = 44$ hectads), east ($n = 27$ hectads) and buffer zone ($n = 85$ hectads) study areas. The overall frequencies of sightings for each species were calculated for each study area as the (number of sightings per species)/(number of sighting locations) and thus differences in sightings frequencies between study areas were determined using a χ^2 test for homogeneity.

To estimate the extent of changes in red and grey squirrel distribution (in km^2) published information on historical distribution (O'Teangana et al. 2000) was used.

Live squirrel trapping

Charleville Forest was selected as a representative site for the midlands area as red squirrel sightings had been reported after an absence of several decades. Grey squirrels were confirmed as being well established historically, with up to 200 squirrels per year removed during periods that control measures were carried out between the 1970s and the late 1990s (David Hutton-Bury, woodland owner, personal communication.). Tomnafinnoge was selected as a control site in the east, as the grey squirrel was reported as having established there in recent years (c.2001). Both woodlands are grey squirrel favourable habitats in that large seeded trees, in particular oak (*Quercus* spp.) are the dominant species present. Both sites are classified as semi-natural woodlands (Fossitt 2000). Charleville Forest (midlands) is approximately 110 ha in size, dominated by mature pedunculate oak (*Quercus robur*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) with a hazel (*Corylus avellana*) understorey. Tomnafinnoge (east) is approximately 70 ha in size and dominated by mature sessile oak (*Quercus petraea*) with some beech, Douglas fir (*Pseudotsuga* spp) and ash, with a hazel understorey and well developed bilberry (*Vaccinium myrtillus*) shrub layer in much of the wood.

In Charleville Forest (midlands), 30 traps were installed at a density of 1 ha^{-1} in three adjacent trapping grids. In Tomnafinnoge (east), 40 traps were installed at a density of 2 ha^{-1} in two adjacent trapping grids. Each trapping session was 8 days long (with the exception of two 7 day sessions). Traps were pre baited for 4 days and set for 4 days at sunrise (but no earlier than 6 am) and then checked after a minimum period of 4 h. In total 16 trapping sessions were carried out in Charleville on a monthly basis from September 2010 to October 2011 (with the exception of December 2010) and then on a bi-monthly basis from January 2012 to May 2012. A total of 7 trapping sessions were carried out in Tomnafinnoge, on a monthly basis from October 2011 to May 2012, with the exception of December 2011.

To determine squirrel density Minimum Number Present was first calculated for each month and then applied to the effective trapping area for each species. In order to determine the effective trapping area, home range radii of 100 m for grey squirrels (Kenward et al. 1998) and 100.9 m for red squirrels (Waters 2012) in deciduous woods were added as a perimeter to the trapping grids. The density range for the red squirrel population in Charleville was compared to density ranges from previous studies on Irish red squirrel populations.

Body size and condition

Body size is expected to have an influence on body mass. In order to remove any such effect, thus to solely examine individual condition, each individual adult was assigned a corrected body mass value (Wauters and Dhondt 1995; Wauters et al. 2000). These values were derived by calculating a linear regression of body mass on shin bone length for the red squirrel population in Charleville ($n = 41$) and the grey squirrel population in Tomnafinnoge ($n = 57$), which was then used to derive residuals of body mass for each squirrel within each population. These residual values were then used as corrected body mass values. The values for the Charleville grey squirrel population ($n = 4$) were derived from the Tomnafinnoge regression equation. Two way ANOVAs were used to investigate variation in condition against sex and trapping month within the Charleville red squirrel and the Tomnafinnoge grey squirrel population. A Mann–Whitney U test was used to investigate whether a significant difference in condition existed between the grey squirrel population in Charleville ($n = 4$ adults) and Tomnafinnoge ($n = 57$ adults). Data from females were then removed and male grey squirrel condition was compared separately. In order to reduce the possible effect that differences in the time of year squirrels were trapped may have had on condition between populations, a further Mann–Whitney *U* test was carried out using data from October to May only.

For comparative purposes, and to investigate for effects (or lack of) of competition on the condition of the red squirrel population in Charleville, the linear regression equation was applied to mean shin bone and body mass measurements obtained from previous studies on Irish red squirrel populations to obtain mean corrected body masss values for these populations. Data was only available for Irish red squirrel populations where grey squirrels have never been present.

Breeding activity was measured by the percentage of adult females in positive reproductive status for each month and breeding rate was measured for each season by the percentage of adult females lactating. A fecundity value for each adult female was determined by calculating the portion of breeding seasons which she was present for, that she was found to show signs of lactation (after Wauters et al. 2001; Gurnell et al. 2004). The population fecundity value was then determined for the grey squirrel population in Tomnafinnoge and the red squirrel population in Charleville as the mean fecundity value for all adult females. The number of weaned juveniles per year was estimated as 1.5 times the number of lactating females (Wauters et al. 1993). Recruitment for the population in Charleville was measured as the number of subadults and new adults recorded between May 2011 and May 2012.

Results

Indirect surveys

A total of 1,136 animal sightings were collected from 835 unique sighting locations between January 2010 and December 2012. Red squirrel sightings ($n = 424$) comprised 37 % of overall sightings, grey squirrel ($n = 264$) 23 % and pine marten ($n = 448$) 40 % of overall sightings at various frequencies throughout the three study areas (Fig. 3).

When the number of sightings per hectad were compared, both pine marten ($\bar{x} = 4.34$, $t = 9.477$, $df = 43$, $p < 0.001$) and red squirrel ($\bar{x} = 4.14$, $t = 8.522$, $df = 43$, $p < 0.001$) were reported from a significantly higher number of locations than the grey squirrel ($\bar{x} = 0.66$) in the midlands. In the east, there was no significant difference between the mean number of red and grey squirrel sightings however the pine marten ($\bar{x} = 2.27$) was reported from significantly fewer locations than either the red squirrel ($\bar{x} = 3.88$, $t = 0.2926$, $df = 25$, $p < 0.01$) or the grey squirrel ($\bar{x} = 4.08$, $t = 2.31$, $df = 25$, $p < 0.05$). In the buffer zone, there were significantly more pine marten ($\bar{x} = 2.13$) than both red squirrel ($\bar{x} = 1.37$, $t = -4.198$, $df = 84$, $p < 0.001$) and grey squirrel ($\bar{x} = 1.4$, $t = -2.722$, $df = 84$, $p < 0.01$).

Paired sample correlation tests for each study area found a positive correlation to exist between the number of pine marten and red squirrel sightings per hectad (midlands $P = 0.678$, east $P = 0.718$, buffer zone $P = 0.572$, $p < 0.001$) throughout the three study areas (Fig. 4). No further correlations between species (i.e. red squirrel and grey squirrel or pine marten and grey squirrel) in terms of sightings per hectad were found.

Species specific differences in sightings frequencies between the three study areas were identified, with significantly more locations having red squirrels reported in the midlands

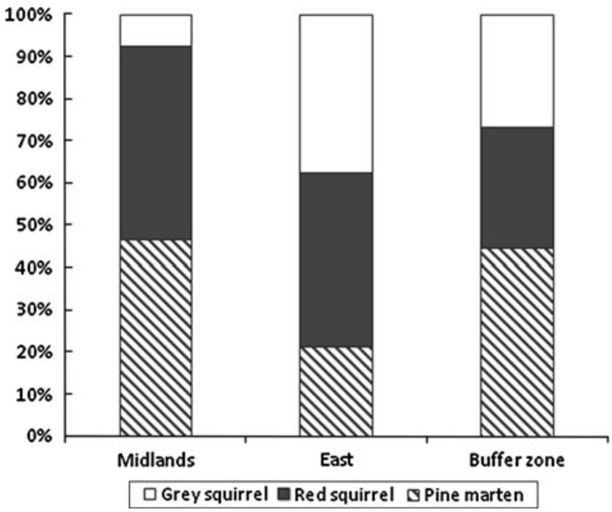


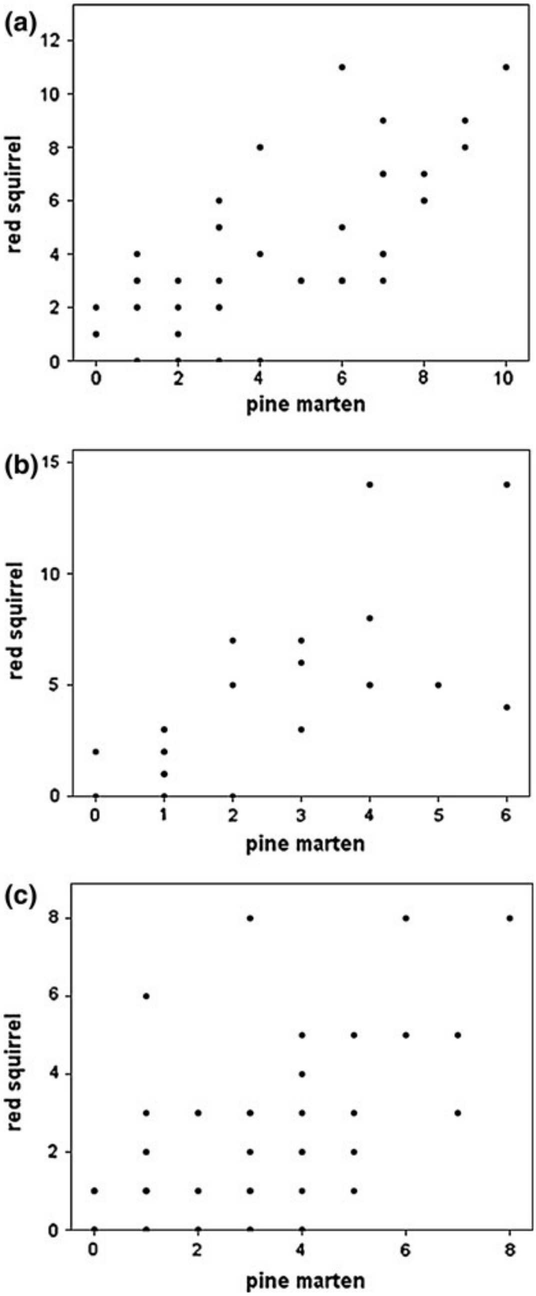
Fig. 3 The percentage of grey squirrel, red squirrel and pine marten sightings in the midlands ($n = 370$ animal sightings in 279 locations, area = 44 hectads), east ($n = 279$ animal sightings in 199 locations, area = 26 hectads) and the buffer zone ($n = 487$ animal sightings in 357 locations, area = 85 hectads)

and in the east than in the buffer zone ($\chi^2 = 17.39$, df = 2, $p < 0.01$). Grey squirrel sightings were significantly fewer in the midlands than in the east or the buffer zone ($\chi^2 = 69.61$, df = 2, $p < 0.01$) and pine marten sightings were significantly fewer in the east than in the midlands or the buffer zone ($\chi^2 = 13.58$, df = 2, $p < 0.01$). Distribution and sightings density patterns for each species based on 10 km radius kernel density are displayed in Fig. 5.

Seventeen of the 18 hairtube surveys were successful in detecting either one or a combination of the target species. In the midlands, only red squirrel and pine marten were detected, whereas in the eastern and buffer zone study areas all three species were detected in various proportions (Fig. 6). The pine marten was found to have a significantly higher detection rate than either the red or grey squirrel in the study as a whole (Wilcoxon's test for matched pairs, $p < 0.05$). A strong negative correlation was found to exist between detection of grey squirrel and pine marten within sites ($r_s = -0.750$, $n = 18$, $p < 0.001$), where only one site (Ballygannon, Wicklow) tested positive for both species ($n = 3/7$ pine marten, $n = 1/14$ grey squirrel). A negative correlation was also found to exist between the detection of red and grey squirrels within sites ($r_s = -0.472$, $n = 18$, $p < 0.05$).

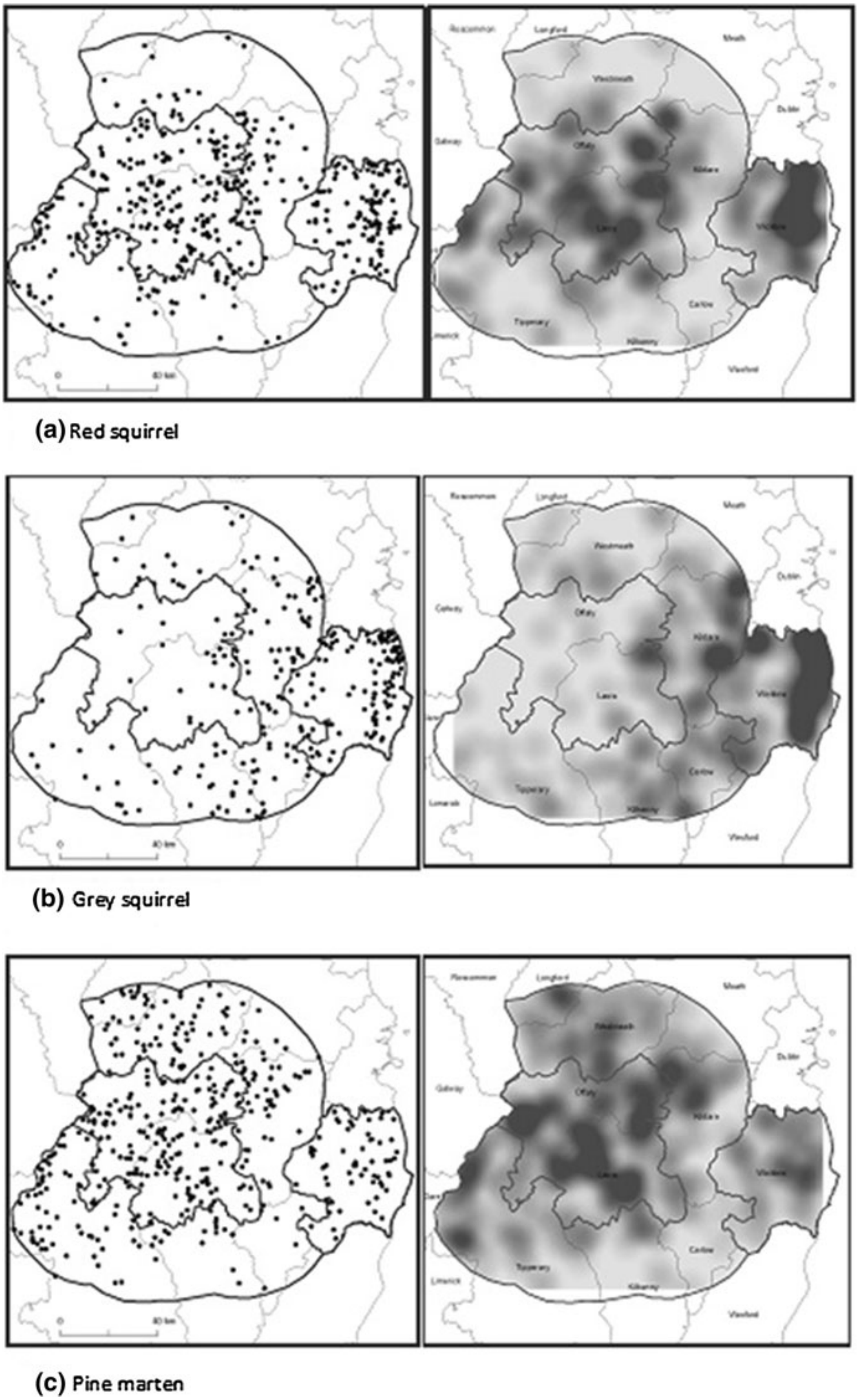
The grey squirrel is now rare in the midland counties of Laois and Offaly and some parts of the buffer zone including North Tipperary and Westmeath (Fig. 5), which accounts for approximately 9,000 km^2 of its former range. The western-most point at which the grey squirrel population is abundant in the study area is east Kildare, and the species is very common in east Wicklow. The red squirrel has naturally recolonised approximately 72 % of the midlands and buffer zone study areas or around 6,500 km^2 of its historic range, and is common and widespread throughout Laois, Offaly and north-west Tipperary. The red squirrel persists and appears to be common in the Wicklow mountains. The pine marten is common and widespread throughout Laois and Offaly, north-west Tipperary, Westmeath and north-west Kildare. There is also a population in the Wicklow mountains. Red squirrel and pine marten populations overlap extensively however grey squirrel and pine marten overlap appears to be limited (Fig. 5).

Fig. 4 Scatter graphs showing correlations between the number of red squirrel and pine marten sighting locations per hectad in **a** the midlands, $P = 0.678$, **b** east, $P = 0.718$, and **c** buffer zone, $P = 0.572$, ($p < 0.001$) study areas



Squirrel population demographics

Red squirrel density in Charleville Forest was consistently higher than grey squirrel density for the duration of the study (Fig. 7). Minimum density of 0.06 ha^{-1} was recorded on the first trapping month i.e. September 2010 and a maximum density of 0.33 ha^{-1} was


(a) Red squirrel
(b) Grey squirrel
(c) Pine marten

◀**Fig. 5** **a** Red squirrel **b** grey squirrel and **c** pine marten distribution and densities throughout the study areas as determined by sightings reported between 2010 and 2012 using sighting locations and 10 km radius kernel density

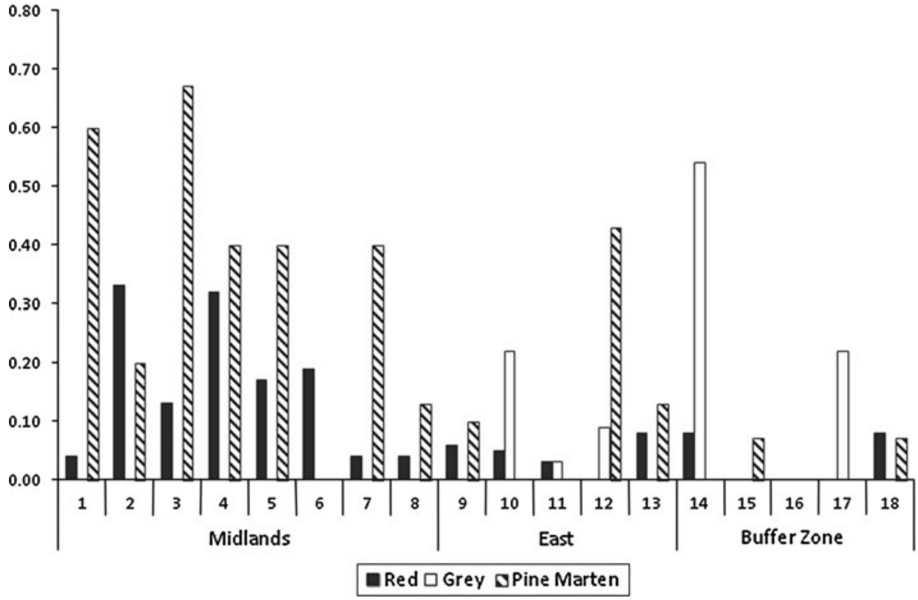


Fig. 6 Proportion of available hairtubes containing red squirrel, grey squirrel or pine marten hair samples from the 18 sites throughout the midlands (Laois and Offaly), east (Wicklow) and buffer zone study areas

recorded in May 2011, with the mean density for the entire study calculated to be 0.23 ha^{-1}. Red squirrels were trapped in all 16 trapping months. Grey squirrels were trapped in 12 of the 16 trapping months.

Grey squirrel density in Charleville Forest ranged between 0 and 0.1 ha^{-1} with a mean value of 0.035 ha^{-1} calculated for the duration of the study. The highest number of grey squirrels found was in the summer of 2011 when 5 squirrels (2 adults and 3 subadults) were known to be present. A total of 4 adult grey squirrels, 3 male and 1 female, were trapped in the course of the study, with the remaining 4 squirrels, all of which were male, being trapped at subadult stage only, in the summer and autumn of 2011 and not again.

Grey squirrel density in Tomnafinnoge ranged from 0.35 to 1.45 ha^{-1} with a mean value of 1 ha^{-1} (Fig. 8). No red squirrels were trapped in Tomnafinnoge.

In Charleville Forest, male red squirrels showed signs of breeding activity in 13 of the 16 trapping months with peaks in February and April/May of 2011 and in January and May of 2012. Between March and October 2011, 9 female red squirrels were trapped whilst lactating, with three of these showing evidence of lactation in both spring and summer months suggesting that they had bred twice in that year. The estimated number of weaned juveniles was therefore 18. From that, recruitment was estimated at 0.67, as there were 5 subadults and 7 new adults captured between May 2011 and May 2012. There was just one female grey squirrel caught over the course of the study in Charleville Forest. She was trapped monthly between May and October 2011, and showed signs of lactation in 4 of the 6 months suggesting that she potentially weaned two litters in 2011. There were 4 subadults caught in the summer of 2011, but not again, and 1 new adult caught in May 2012.

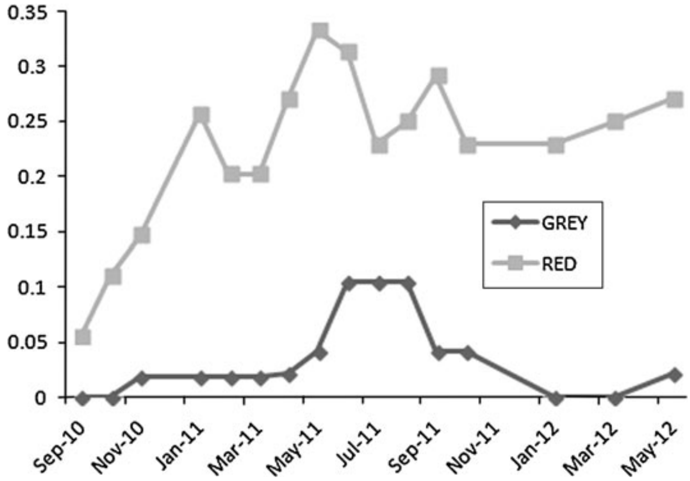


Fig. 7 Red and grey squirrel densities in Charleville between September 2010 and May 2012 as determined by minimum number present

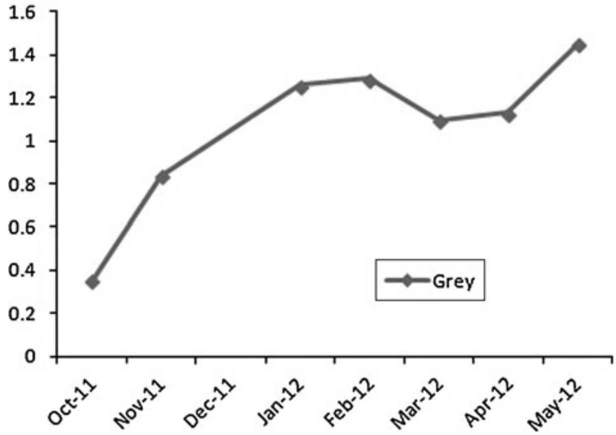


Fig. 8 Grey squirrel density in Tomnafinnoge between October 2011 and May 2012 as determined by minimum number present

In Tomnafinnoge, male grey squirrels showed signs of breeding activity in each of the 7 trapping months, peaking in January and in particular May, when all 26 adult males trapped showed signs of breeding activity. Female grey squirrels in Tomnafinnoge also showed signs of breeding activity in each trapping month, with peaks in February/March and again peaking in May when 14 of the 15 adult females trapped were lactating. The trapping period of 7 months was not long enough to identify new adults in the population. Data gathered on the reproductive success of the populations from both woods are described in Table 1. As the study period in Tomnafinnoge was less than 1 year, not all parameters could be measured.

Mean adult red squirrel shin bone length ranged from 60.98 to 71.7 mm ($n = 41$, $x = 68.19 \pm 0.7$, 95 % CI) in Charleville forest, and there were no significant differences between male and female squirrels ($F = 0.486$, $p = 0.49$). Adult grey squirrel shin bone length in Charleville Forest ranged from 75.4 to 80.3 mm ($n = 4$, $x = 77.85 \pm 3.46$, 95 % CI). Mean adult shin bone length in Tomnafinnoge ranged from 74.6 to 79.7 mm ($n = 58$, $x = 77.04$, $\pm$ 0.3, 95 % CI) and likewise no significant differences between the sexes were found ($F = 0.56$, $P = 0.46$).

The linear regression equations for Charleville and Tomnafinnoge and mean corrected body mass values for adult male and female squirrels are described in Table 2. Overall adult red squirrel values in Charleville ranged from −40 to + 31.9 ($\bar{x} = -0.03 \pm 5.41$, 95 % CI, $n = 41$). A two way ANOVA found no significant variation in condition between the sexes or trapping months in the Charleville red squirrel population ($F = 0.905$, $P = 0.556$). In Tomnafinnoge, corrected body mass values ranged from −72.11 to 71.18 ($\bar{x} = 0.019 \pm 9.54$, 95 % CI, $n = 57$). Overall adult female grey squirrels were in significantly better condition than males ($F = 31.837$, df = 1, $p < 0.001$) and condition in January was significantly higher regardless of sex ($F = 2.203$, $p < 0.05$, df = 6).

Despite differences in sample size, the Charleville adult grey squirrels ($n = 4$) were found to be in significantly poorer condition than those in Tomnafinnoge ($n = 57$) ($U = 25$, $p < 0.006$), and when tested separately, the males ($n = 3$ and $n = 33$) even more so ($U = 3$, $p < 0.002$). When data from October to May only were used the difference in condition was still significant between the populations ($U = 9$, $p < 0.003$) suggesting that the observed difference in condition between the populations is not a result of differences in the time of year that populations were trapped.

Discussion

Squirrel distribution

The grey squirrel is now rare in much of the midlands region of Ireland. Grey squirrel sightings accounted for less than 8 % of animal sightings in this region, which is remarkably low considering that they are a much less elusive species than either the red squirrel or the pine marten, and are also more commonly associated with human settlements. A total of 28 grey squirrel sightings were received over the 3 year study which were all infrequent or one-off sightings and thus not representative of normal populations. It is not possible to infer absolute absence with the technique used, however relative detectability of the species is clear.

The findings of the hairtube surveys further support those of the sightings survey, in that the grey squirrel was not found to be present in detectable levels at any of the midlands sites. Information gathered from woodland owners, foresters and gamekeepers indicated that occasional, localised control programs had taken place historically at some sites. However, culling programs at the scale that would be necessary to suppress the midlands population have never been carried out. In fact, the most recent grey squirrel control program in any of the midlands hairtube survey sites was carried out more than 10 years ago. Thus it is unlikely that culling has been an influencing factor in shaping contemporary grey squirrel distribution in the midlands.

In contrast to the grey squirrel, the red squirrel and pine marten were common and widespread throughout the midlands and each accounted for 46 % of sightings in the region. When survey respondents who had lived in the midlands study area for more than 2 decades were questioned, it appeared that the red squirrel had begun to recolonise from the late 1990s onwards. Whilst information on the timing of this phenomenon may be

Table 1 Sex ratios, reproductive activity and recruitment for the red and grey squirrel population at Charleville and the grey squirrel population at Tomnafinnoge

	Charleville Sept 10–May 12	Charleville Sept 10–May 12	Tomnafinnoge Oct 2011–May 12
Species	Red	Grey	Grey
N	45	8	71
Sex ratio (% M)	0.68	0.82	0.55
Subadults trapped			
2011	5	4	Na
2012	0	0	10
New adults trapped			
2012	7	1	Na
Litters			
2011 (all year)	12	2	Na
2012 (first half of year)	4	0	19
Fecundity	0.59 (±0.21, 95 % CI)	Na	0.87 (±0.13, 95 % CI)
Breeding rate (F)			
Spring 2011	62.5 %	Na	Na
Summer 2011	87.5 %	Na	Na
Spring 2012	50 %	Na	91 %
No. of litters per female in 2011			
0	25 %	Na	Na
1	50 %	Na	Na
2	25 %	Na	Na

Breeding rate was calculated as the percentage of adult females that were lactating for each season. Population fecundity was calculated as the mean fecundity value for all females after individual fecundity was calculated as the portion of breeding seasons that each female was present for in which signs of lactation were observed

Table 2 Fitness values (±95 % confidence intervals) calculated as residuals from regression equations on body mass versus shin bone length for adult male and female red squirrels in Charleville and Tomnafinnoge

Site and species	Linear regression	Mean fitness F	Mean fitness M
Charleville—red	$y = 4.601x - 22.261$	1.44 (±3.018, $n = 19$)	−1.31 (±7.42, $n = 22$)
Tomnafinnoge—grey	$y = 21.065x - 1042.4$	15.68 (±14.06, $n = 24$)	−11.37 (±11.82, $n = 33$)
Charleville—grey	As per Tomnafinnoge	−22.42 ($n = 1$)	−87 (±90.38, $n = 3$)

anecdotal, the sightings and hairtube survey results provide unequivocal evidence that the native red squirrel is now common and widespread in the region, which was once dominated by the introduced grey squirrel. This process has occurred naturally without any significant human intervention or management of either squirrel species.

Species distributions in the east were significantly different to those in the midlands. In the east both the red and grey squirrel were reported in similar frequencies and the pine marten less frequently than either squirrel species. Hairtube survey results also revealed differences in distribution and various combinations of the three species were detected across the eastern sites as opposed to only red squirrel and pine marten in the midlands sites. One site in the east detected both grey squirrel and pine marten and this represented the only hairtube survey site in the entire study which detected both species together. Thus the pine marten and grey squirrel were found to have a strong negative correlation in detection at woodland level across the study areas. A negative, albeit weaker, correlation was also found to exist between the red and grey squirrel in terms of detection at woodland level, as would be expected due to the effects of competition.

The buffer zone study area appears to be divided between regions where pine marten were frequently reported (north and south west of the buffer zone) and regions where grey squirrels were frequently reported (east and south east) (Fig. 5). The decline in grey squirrel range and recolonisation by the red squirrel population falls entirely within the core range of the pine marten population in the midlands and buffer zone study areas. Since the grey squirrel's introduction to Ireland, the river Shannon has represented the western most extent of their range (O'Teangana et al. 2000). The current study has found the western boundary of an abundant grey squirrel population in the study area is now in the region of Kildare and Carlow, which represents a shift of more than 100 km east and around 9,000 km^2 in terms of land coverage within the overall study area. This shift eastwards also suggests the Shannon, although undoubtedly important as a physical barrier, may not have been the sole barrier to the spread of the grey squirrel into the west of Ireland.

Squirrel demographics

In both their natural range in the eastern United States, and their introduced range in Ireland, Britain, Italy and Canada, normal grey squirrel density is several squirrels per hectare in large seeded broadleaved woods (Thompson 1978; Gurnell 1996; Kenward et al. 1998; Don 1983; Gurnell et al. 2001b; Lawton and Rochford 2007). The grey squirrel density of 0.035 ha^{-1} recorded in Charleville is therefore atypical for the species, particularly considering they had been established in the woodland since the 1960s. In contrast, the red squirrel population is living at normal density, despite a previous absence from Charleville of more than 30 years.

Table 3 Fitness values and density ranges for Charleville* and various other red squirrel populations in Ireland where grey squirrels were not present (fitness values derived from reported mean body weight and shin bone length using the regression equation from adult red squirrels in Charleville: $y = 4.601x - 22.261$)

Habitat type	Mean fitness value	Density range	Study
Coniferous	+5.53	0.21–0.39	(Reilly 1997)
Coniferous	+4.07	0.02–0.11	(Reilly 1997)
Broadleaf	−0.03	0.20–0.33	Charleville*
Mixed broadleaf	−5.02	0.24–0.44	(Waters 2012)
Coniferous	−19.68	0.21–0.34	(Waters 2012)
Mixed	−24.91	0.35–1.02	(Poole 2007)

Although the effects of competition are notoriously difficult to measure, several long term studies on sympatric red and grey squirrel populations, compared to "red squirrel only" sites, have identified the population parameters by which the effects of interspecific competition can be measured. As such, decreased juvenile recruitment (Wauters et al. 2000), and reduced fitness leading to reduced fecundity (Gurnell et al. 2004) in the red squirrel population have been found to be key factors in the usual replacement of red squirrels by greys, in particular in oak dominated habitat (Kenward et al. 1998) such as Charleville. During this study however, red squirrel population demographics did not indicate that there was any significant competitive pressure from the sympatric, low density, grey squirrel population. For example, the population fecundity value of 0.59 is more comparable to the value of 0.62 (found in a "red-only" population in north Italy) than 0.48 (found in a "red-grey" population in the same study) (Gurnell et al. 2004). Similarly, the breeding rates of 62.5 and 87.5 % for spring and summer 2011 respectively in Charleville were more typical of the "red-only" site in the north Italy study as opposed to the "red-grey" sites, where summer breeding in particular was significantly lower.

Red squirrel density and red squirrel condition in Charleville were also comparable to those of several other Irish red squirrel populations where grey squirrels had never been present (Table 3). Red squirrels would typically be expected to have lower densities than grey squirrels where their populations do overlap, but this is clearly not the case for the population in Charleville, where mean red squirrel density of 0.23 ha^{-1} was more than six times greater than mean grey squirrel density during the course of the study.

In contrast, the grey squirrel density of 1 ha^{-1} recorded in Tomnafinnoge is typical of expected densities for this type of habitat in Ireland (Lawton and Rochford 2007), and is >28 times greater than that of grey squirrel density in Charleville. While there was only one female grey captured throughout the entire study period in Charleville, there were 29 females captured in Tomnafinnoge, despite the shorter study period, with an estimated 19 litters born, and a population fecundity value of 0.87.

When the condition of the grey squirrel population in Charleville was compared to the population in Tomnafinnoge, significant differences were found. Whilst body size values were very similar between the two populations, there was a considerable difference in body mass, thus the corrected body mass values for the adult grey squirrels in Charleville, in particular males, were found to be in significantly lower than those in Tomnafinnoge as a result ($p < 0.002$), despite the difference in sample size. Adult females in Tomnafinnoge were also found to be in significantly better condition than their male counterparts, however this is likely to have been influenced by a greater body mass in gestating females, as 91 % of adult females showed signs of breeding activity at the time they were captured.

Notably, the four subadult grey squirrels that were captured in the summer of 2011 in Charleville were never detected again, suggesting they had either dispersed from the woodland, or died. This is unusual considering that the population is well below the normal carrying capacity, and as such recruitment of subadults into the population should be high.

The overall health and status of the grey squirrel population in Charleville was extremely poor, in stark contrast to the population in Tomnafinnoge who are thriving. Woodland size and tree species composition are very similar between the two woods, suggesting habitat quality is not a contributing factor. It is evident from this study that the red squirrel population is co-existing with this low number of greys, without any evidence of competitive pressure from their invasive counterparts. The red squirrel population in Charleville is therefore in competitive release from the grey squirrel, in a woodland where it had once been considered locally extinct.

Pine marten abundance

A recent study by Sheehy et al. (2013) investigating pine marten abundance and diet in the midlands and eastern study areas found an average of 3.13 adult resident pine marten present per km^2 of forested habitat surveyed in the midlands, compared to 1.01 per km^2 in the east (where present). The difference in abundance between the midlands and eastern study areas further corroborates evidence in the current study that the pine marten population in the midlands is considerably more advanced in their recovery than the population in the east. At woodland level, abundance values for Charleville and Tomnafinnoge were 4.42 and 1.25 adult resident pine marten per km^2 respectively.

It is possible that the high density predator population in Charleville may be influencing foraging behaviour, body condition, reproductive activity or density in the grey squirrel population. It is also possible that the critical breeding weight is not being reached, which results in reduced breeding activity, leading to reduced recruitment of juveniles into the population. There was only one adult female captured during the Charleville population study however, and it is therefore not possible to deduce that adult females are not reaching a critical breeding weight from that one individual. Indeed, that individual was within the normal weight range and showed signs of successfully breeding twice in 2011, although none of her offspring were recruited into the population.

Sheehy et al. (2013) found no evidence of pine marten predation on grey squirrels in any of the scats collected in the midlands sites, where grey squirrels are scarce, but did find that they were preyed upon by the low density pine marten population in the east. Red squirrels were rarely preyed upon even when available in relatively high numbers. Despite this apparent higher rate of predation on the alien squirrel species, it would be unlikely that a low density pine marten population could impact a high density grey squirrel population by direct predation alone. Indeed the grey squirrel population in Tomnafinnoge appear to be thriving despite the presence of a low density pine marten population. Thus in order to establish the nature of the relationship between the native predator and invasive squirrel species, observing the effects of an increase in pine marten density on an established grey squirrel population will be fundamental.

Population crashes in formerly invasive species

This is the first documented evidence of a grey squirrel population retracting, without any human intervention, subsequent to having established itself as an invasive species. In a review of population crashes of established introduced species, Simberloff and Gibbons

(2004) define a "population crash" as one in which numbers or densities were believed to have fallen by at least 90 % in less than 30 years. Under this criterion, the grey squirrel population of the midlands region can also be described as having undergone a "population crash" based on a density of 0.035 squirrels ha^{-1} (compared to a population density in the east of at least 1 squirrel ha^{-1}). However, as the current study found the population in the east of the country to be doing well, and a recent sightings and hairtube survey has confirmed that the grey squirrel continues to spread into the south and south west of the country (unpublished data from Goldstein et al.) the population crash must also be described as regional.

In their review, Simberloff and Gibbons found that such population crashes are not a common phenomenon, they have rarely been studied experimentally or quantitatively, and the causal factors often remain unidentified. Furthermore whilst quantitative data documenting perceived declines were exceedingly scarce, even more so was evidence as to how or why such population crashes came about, as the majority of proposed explanations were simply ad hoc suggestions with no actual supporting evidence. Simberloff and Gibbons discussed seventeen examples including invasive vertebrate, invertebrate and plant species' decline. Causal factors were suggested including competition with (subsequently) introduced species, parasitism by subsequently introduced species, exhaustion of resource, and one case of adaptation by a native herbivore, however in the majority of cases the cause remained entirely unknown.

In considering possible reasons for the grey squirrel's regional decline in Ireland, certain theories can be ruled out with certainty, for example, competition with a subsequently introduced species. In Ireland the only species with which there is any significant competition for resources is the native red squirrel. Under normal circumstances, the grey squirrel is a superior competitor and inevitably outcompetes the red squirrel for resources (MacKinnon 1978; Wauters et al. 2000; Gurnell et al. 2004).

Squirrel numbers in any given year have been found to be closely linked with the previous year's tree seed crops (Gurnell 1983), and population densities fluctuate on a yearly basis in accordance with both tree seed crops and winter temperatures (Gurnell 1996). Exhaustion of resource or food scarcity can be ruled out for two reasons. Firstly, there has been no evidence of a tree seed crop failure in Ireland, nor specifically in the midlands region, that could conceivably lead to such a prolonged drop in grey squirrel numbers. Indeed, habitat analysis (unpublished data from Sheehy) in Charleville Forest confirmed there was an abundance of tree seeds available in 2010 and 2011. Secondly, the red squirrel population were confirmed to be in good condition, with body condition index, breeding and recruitment all within the healthy range. Any impact of food scarcity, current or historic should in theory have also impacted the red squirrel. The evidence gathered in the course of the current project on both grey squirrel and pine marten distribution and Sheehy et al.'s study (2013) on abundance suggest that the success or failure of the grey squirrel population in Ireland may be linked to pine marten abundance more so than distribution alone.

Historically, the grey squirrel has never established itself in the core range of the Irish pine marten population in the west, despite its close proximity to their point of introduction. The river Shannon has traditionally been considered a barrier to the grey squirrel's dispersal into the West of Ireland as the eastern banks of the Shannon were historically the western most extent of the grey squirrels range. Although this significant physical barrier could hinder the progression of the invasive species range expansion, it is unlikely to be the sole cause of the grey squirrel's failure to colonise the west of Ireland. Grey squirrels are capable of swimming (Koprowski 1994), and have crossed other large rivers in Ireland

(Carey et al. 2007). Furthermore, several areas along the banks of the river Shannon exist at which a squirrel could cross via the tree canopy from one side to the other. Carey et al. (2007) proposed that the lack of suitable habitat west of the Shannon was more likely to explain the failure of the grey squirrel to establish there, despite having crossed the river on several occasions. Whilst the lack of favourable habitat is likely to have contributed towards the grey squirrel's failure to establish in the west, it does not account for the failure to disperse westwards north of the source of the Shannon, where moderately and highly favourable habitat for dispersal exists.

It is plausible now to suggest that the failure of the grey squirrel to establish in the west may also be related to historic pine marten distribution. O'Sullivan (1983) described the pine marten population in Ireland in the mid twentieth century (the time at which the grey squirrel population was expanding) as being restricted to the west of the river Shannon, from Limerick to Sligo. Indeed distribution maps in both O'Sullivan (1983) and O'Mahony et al. (2012) indicate that the limit of the pine marten's range in the west both currently and historically reaches north of the source of the Shannon, and thus could well have been an inhibitor to the spread of the invasive species through this corridor of suitable habitat.

As the pine marten population has expanded from the west and the Slieve Bloom mountains, grey squirrel range has retracted. O'Teangana et al. (2000) described the grey squirrel as ubiquitous in the midlands, although they did note it was not doing as well as expected in the Cavan/Monaghan region (north of the midlands region in the current study). Carey et al. (2007) showed the grey squirrel had begun to noticeably decline in the midlands between 2000 and 2007. The results from the current study clearly show the grey squirrel population in the midlands had in fact collapsed by 2012. It was not until Carey et al. reported the decline in the Laois Offaly region in 2007 that the pine marten was implicated as a possible factor in the grey squirrel's decline. Interestingly, O'Mahony et al.'s National Pine Marten Survey in 2006, published around the same time as Carey et al. (2007)'s Irish Squirrel Survey, illustrated the expansion of the pine marten population from the core range west of the Shannon (and a smaller population in the Slieve Bloom mountains in Laois and Offaly) into the greater midlands area. This expansion occurred, probably very gradually, between the 1980s and 2007 however the exact timing has not been documented. Nonetheless, the current study has confirmed that by 2012 there was an abundant native pine marten population in the midlands of Ireland, and only the highly reduced remnants of a once abundant alien grey squirrel population persist.

Implications for the rest of Ireland, Britain, and Europe

Although evidence thus far has been anecdotal, it has also been suggested that a similar phenomenon is occurring in Scotland, where the pine marten is present and expanding, to that which has occurred in Ireland (Paterson and Skipper 2008). Furthermore, the grey squirrel has flourished (at the expense of the native red squirrel) in the absence of a pine marten population in England and Wales where habitat loss and particularly human persecution are believed to be responsible for what is now described as a "functionally extinct" pine marten population. It is possible that the absence of the native squirrel predator has allowed the alien squirrel species to become hyper-successful since its introduction in the nineteenth century.

It is possible that the current range expansion of the pine marten in Scotland (Croose et al. 2013) could perhaps result in the eventual re-establishment of a pine marten population in England and Wales. However whether the pine marten population will reach similar densities to those of the Irish population remains unknown, as does whether they might cause a subsequent decline in the numbers or range of the invasive squirrel species.

In Italy, the grey squirrel has also successfully established as an invasive species, and has caused the local extinction of native red squirrel populations. Since their introduction near Turin in 1948, they have spread to an area greater than 2,000 km^2, and subsequently the red squirrel population has undergone local extinction in c. sixty-two percent of that area (Bertolino et al. 2013). The grey squirrel is now also spreading into the hilly region of Piedmont, approaching Alpine valleys where continuous forest cover may facilitate both an increase in the population range and the rate at which they spread. This represents a serious threat to the long term survival of the red squirrel in Europe, as the dispersal of the grey squirrel beyond the Italian border could lead to the continued spread throughout mainland Europe to the detriment of the red squirrel (Lurz et al. 2001; Bertolino and Genovesi 2003; Bertolino et al. 2008, 2013).

Recent studies have found the pine marten population in the region of Piedmont may also be increasing (Balestrieri et al. 2010). The pine marten in this area is typically associated with forests situated between 1,000 and 2,000 m above sea level however roadkill pine marten have recently been reported in nearby lowland agricultural landscape. Population densities in the region are not known but Italian pine marten numbers appear to be low from the records to date (0.34 pine marten km^2) (Manzo et al. 2012). This is considerably lower than pine marten density in the midlands, and is also lower than the east of Ireland, where the grey squirrel population is still doing well. Similarly to Britain, it is not known what population density the pine marten could potentially reach in Italy, as the historic decimation of predator populations means information on contemporary density capacities are unavailable. The potential role of the Italian and indeed the Swiss and French pine marten populations in preventing the spread of the grey squirrel further into mainland Europe therefore also remains unknown.

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