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Research Article

The changing patterns in the distribution of red and grey squirrels in the North of England and Scotland between 1991 and 2010 based on volunteer surveys

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Abstract

In the UK, alien grey squirrels have been replacing the native red squirrel for more than 100 years and by the turn of the century the distribution of grey squirrels had extended to most of central and southern England and Wales (apart from some islands), and large parts of Scotland and Ireland. To understand how this species replacement may continue into the future, we explore 20 years of squirrel records (1991-2010) collected in an unsystematic way by volunteers in northern England and Scotland. To aid analysis, we standardised the data to one record of squirrel presence per 4 km square per year in each of six geographic regions, two in northern England and four in Scotland. Over the 20 years and across all regions, the number of 4 km squares that returned the presence of squirrels increased from 23% to 80%. The evolving distribution pattern of red and grey squirrels differed among the regions and was complex with occupancy records for many 4 km squares changing from red to grey squirrel from one year to the next, but also some changing from grey to red squirrel. The net rate of change, however, was from red to grey squirrel with the exception of the more recent years, 2007-2010, when this trend became less distinct. Estimates of the complete loss of red squirrels assuming current trends, varied from the 2020s in northern England to 2104 in North East Scotland. The recent incertitudes in the replacement of red by grey squirrels may, at least in part, result from increasing efforts to control grey squirrels in these regions. Although the volunteer data presented are valuable, monitoring aims must be clearly defined and sampling designs involving volunteers and professionals must be systematic and of sufficient effort to obtain reliable information on changes in distribution and population trends.

Introduction

The grey squirrel was first introduced to Britain in 1876 at Henbury Park in the county of Cheshire as an attractive, exotic animal, and within a period of about 50 years there were several further introductions and translocations within the country (Middleton, 1930; Parsons and Middleton, 1937; Shorten, 1954). The grey squirrel spread from these first points of introduction, replacing the native red squirrel and causing damage to timber crops in the process. Interspecific competition (Wauters and Gurnell, 1999; Wauters et al., 2000, 2005) and an emerging infectious disease, squirrel pox virus, carried by grey squirrels and lethal to red squirrels, are believed to be responsible for the replacement of red by grey squirrels (Tompkins et al., 2003; Carroll et al., 2009; Bruemmer et al., 2010; McInnes et al., 2013). In Ireland the picture was similar although there was just one point of introduction in the middle of the country at Castle Forbes, County Longford in 1911 (Carey et al., 2007).

Early studies on the changing distribution of red and grey squirrels nationally were reviewed by Lloyd (1983) and more recently regional accounts have been published for Cumbria (Lowe, 1993, 2007; Lurz et al., 2005), the North of England and the Borders (Lurz, 1995), Scotland (Usher et al., 1992; Bryce, 1997; Lurz, 2010) and Ireland (Carey et al., 2007).

To understand recent trends in the replacement of red by grey squirrels in northern England and Scotland we explore here a data set collected largely in an uncoordinated way by volunteers between 1991 and 2010. Records of squirrel presence stem from a wide range of sources such as squirrel sightings from bird feeders, random encounters in parks and woodlands, road kills, or grey squirrel control operations. There was no consistency of effort (in time or space), nor were populations closed or sites necessarily independent. The data therefore do not conform to assumptions of available model frameworks (e.g. MacKenzie et al. 2002, 2009) and we have deliberately chosen a simple approach to data analysis to investigate what information can be gleaned from public records, accepting they represent in fact a true underestimate of the likely presence of a species. Despite data deficiencies, we explore more than 49000 records to see if any trends in the distribution of the red and grey squirrels over the study period would be revealed. This paper represents the first analysis of overlapping distribution data of red and grey squirrels at national and regional scales since Usher et al. (1992) and Bryce (1997) in Scotland and Lloyd (1983) in England.

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Methods

The data

The recent distribution data on red and grey squirrels in the North of England and Scotland started to be collected in 1985, but the number of records were few in the early years and therefore this study covers the period from 1991 to 2010 inclusively. The records were made by members of the general public or volunteers in response to requests by red squirrel conservation and other organisations, in particular: Tullie House Museum, Cumbria Wildlife Trust, Northumberland Wildlife Trust, Yorkshire Mammal Society, Forestry Commission Kielder Forest District, Red Squirrels in South Scotland, Scottish Wildlife Trust

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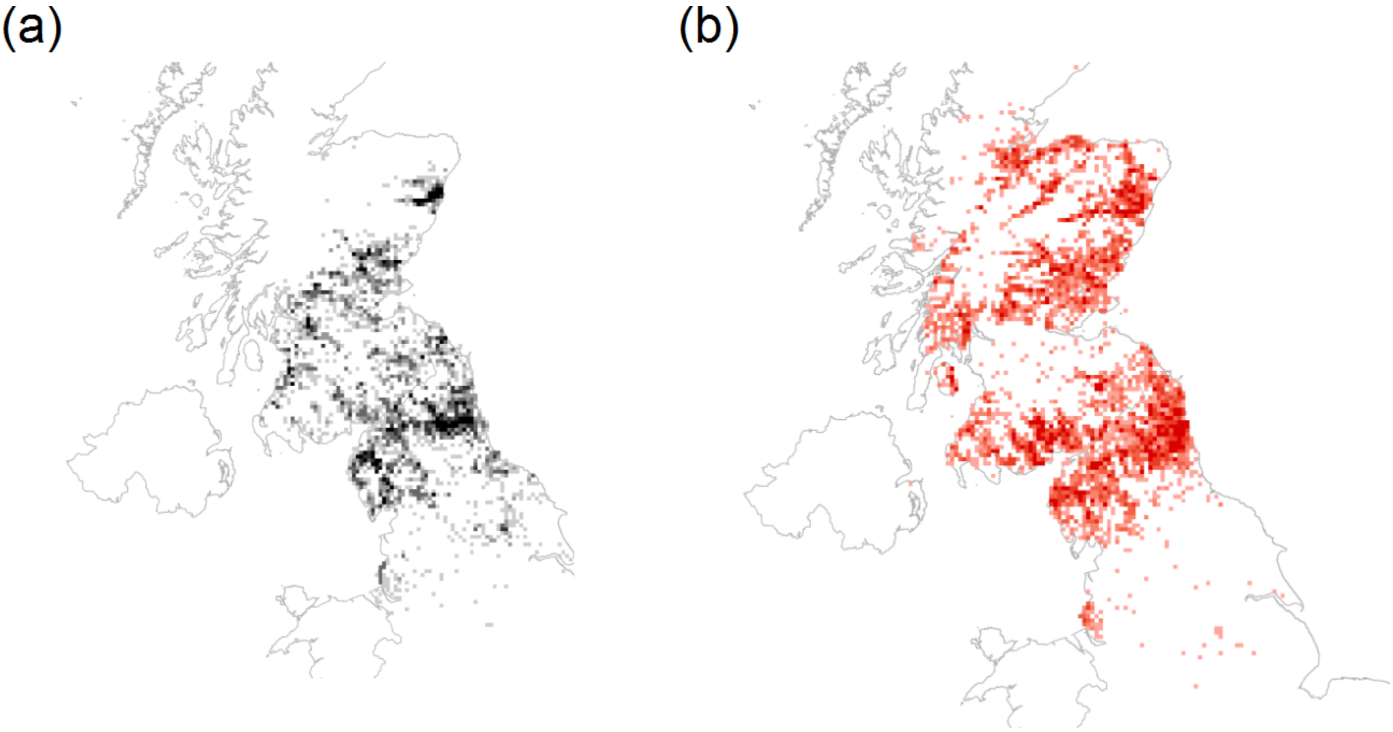

Figure 1 – Dot maps of the distribution of records of squirrels in the north of England and Scotland for the years 2004-2009 based on 4 km squares. (a) grey squirrels, (b) red squirrels.

and the Westmorland Squirrel Group. For the most part, the surveys were not systematic, of varying effort and location information which was supplied with the records was not standard and varied from "the nearest town or village", to a post code or a grid reference. Associated information included date but information such as habitat were inconsistently noted. We have collected the records in electronic format and compiled them without targeting specific areas or years. Many records were not checked at the time of collection. Where possible, therefore, we have verified the records from other information supplied with the records, although species misidentification (see Gurnell et al. 2009) cannot be ruled out. We selected a 4-km resolution to provide sufficient detail to identify patterns in the changing distributions of red and grey squirrels. Therefore, we removed records >4 km resolution. Any records that were implausible were also removed (e.g. squirrels in the sea etc.). Records spanned all months of the years, so to further standardise the data, we filtered them to produce one record per 4-km square per year for each year in the 20-year period. For each year and square, the records consisted of red squirrel presence, grey squirrel presence, both species present, or neither species present. As an example, the pooled records for 2004-2009 are shown in Fig. 1. With this degree of data distillation, the reasons why the original records were made (e.g. sightings made on a casual basis, sightings at a bird feeder, road kill, grey squirrel control) is of no relevance to the analysis.

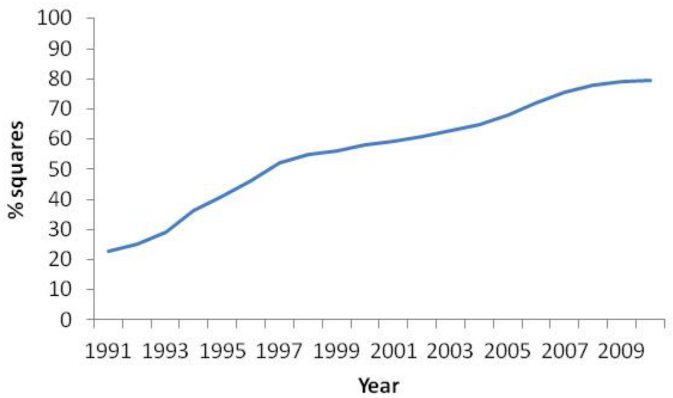

Figure 2 – Percentage of squares (N=2625) in the counties of Cumbria and Northumberland in the north of England, and Scotland, excluding the Scottish Highlands, reported each year over the study period, 1991-2010.

Overall, there has been a marked increase in records over the time period, from 23% of all squares to 80% (Fig. 2) as more and more volunteers responded to requests for information. The geographical coverage of the data was uneven and inconsistent from year to year, that is, square occupancy was only recorded in some years and not others. This contrasts to the frequently adopted method of targeting specific areas or squares and, through direct observation or questionnaire, recording presence data at specific times (e.g. O'Teangana et al. 2000).

The data were not suitable to look at the effects of habitat composition or other factors on the changing distribution patterns, but, since squirrels are arboreal animals, we looked at the level of forest cover at which squirrels were first detected. For this, we used Corine Land Cover 2000 raster data (as provided by the European Environment Agency). These data are appropriate for our study since tree plantings after the year 2000 would be too young to support squirrels. The three forest classes (conifer, deciduous, and mixed forest) have been used to produce a total forest cover map, on the same 4-km grid used for the squirrel data. The total area of forest in the north of England and Scotland is not high, and forests tend to be fragmented. The mean percentage forest cover per square across the whole study area was 11.2% (N=2625, sd=16.81) and with a median of 4.5% (Interquartile Range = 14.0); the distribution was highly overdispersed (Index of Skewness = 2.17). We allocated squares to six categories of increasing levels of % forest cover: 0, 0-2, 2-5, 5-10, 10-25 and 25-100 to produce a reasonably even number of squares in each category, although most squares were in the zero forest cover category. We then calculated the mean number of records from the 20 year data set for each % forest cover category.

Study area

Distribution maps were produced using ESRI ArcGIS 9.2, importing each record as a point and then allocating each "year point" to each 4-km cell. To help us understand differences in trends across the geographic area, we have stratified our analysis on the distribution records in six geographic regions (Fig. 3).

Figure 3 – Regions used in the analysis of squirrel distribution records. Map also shows the counties of Yorkshire and Lancashire and the National Trust Red squirrel Reserve at Formby.

Although red squirrels are still present in some parts of Lancashire, in particular around the National Trust Reserve at Formby (Figs. 1, 3), and in Yorkshire (e.g. Court and Fawcett 2008), we have concentrated our analyses in the north of England on two counties, Cumbria (C) (426 4-km squares) and Northumberland (ND) (350 4-km squares). These two counties have been the focus of a much red squirrel conservation work in the last 20 years (e.g. Lurz et al. 1995, 1998, 2005; Venning et al. 1997; Wauters et al. 2000; Gurnell et al. 2004, 2009; Parrot et al. 2009).

In Scotland, we have looked at the records in four regions, but not those in the Scottish Highlands where only red squirrels have been recorded at the time of writing (Fig. 3). Grey squirrels were introduced near Loch Long in the western part of the Central Lowlands in Scotland in 1892 and in Dunfermline in the eastern part of the Central Lowlands in 1919 and Edinburgh in ca. 1913 (Middleton, 1930, 1931), and they had spread throughout much of the Central Lowlands by the early 1980s (see Shorten 1954, 1957; Lloyd 1983). To look at the more recent records we have divided the Central Lowlands into two approximately equally sized regions; Central Lowlands West (CLW) (430 squares) and Central Lowland East (CLE) (378 squares) (Fig. 3). The fifth region is the South of Scotland (SS) (795 squares) which has been subject to grey squirrels encroaching both from the north and from England in the south in recent years. The final region is the north east of Scotland (SNE) (246 squares), in particular around the city of Aberdeen, where grey squirrels have been recorded for about 30 years (Lloyd, 1983; Staines, 1986).

Analysis

The squirrel presence data assembled here have been collected in an unsystematic way and are not suitable for such analytical methods as ecological-niche factor analysis (ENFA; Hirzel et al. 2002) or occupancy analysis (MacKenzie et al., 2002; MacKenzie and Royle, 2005). Moreover, we have arbitrarily imposed time (1 year) and spatial units (4-km squares) to simplify the data, but these were not part of any preconceived survey design. With the knowledge that red squirrels were at one time universally distributed throughout the British Isles, and that the invading grey squirrel has been inexorably expanding its range and replacing the red squirrel (e.g. Shorten 1954, 1957; Gurnell et al. 2012), we have made some simplifying assumptions about the data before analysing trends in square occupancy.

Assumptions

1. That any square that had no record for a particular year or run of years would remain with the stated occupancy of the last recorded year. For example, a run of 10 years for a square that was: RRNNRNGGNG would become RRRRRRGGGG (where R = red squirrel present, G = grey squirrel present, N = neither species recorded as present and B = both species present).
2. Because the number of recorded squares were very low at the beginning of the study period, we have assumed that all squares at the beginning of the period in 1991 were occupied by red squirrels, unless they were actually recorded to be occupied by grey squirrels or both squirrel species. This is a reasonable assumption for all regions where there were few grey incursions at the beginning of the period, except for the Central Belt and Fife in Scotland where grey squirrels had been introduced some 100 years ago (Loch Long 1892, Edinburgh ca. 1913, Fife 1919; Middleton 1930). To try and improve the information on recorded presence of grey squirrels for 1991 we further adjusted the records for 1991 using information from the Forestry Commission Annual Squirrel Questionnaire Reports (unpublished internal Forestry Commission reports). These questionnaires were completed annually by forest managers who recorded the presence or absence of red or grey squirrels in state-run forests in 10-km National Grid squares between 1973 and 1995. We recorded the questionnaire occupancy for any of our 4-km squares that overlapped 50% or more with a 10-km square. This increased the number of grey squirrel records for 1991, particularly for the Central Lowland regions. However, since the geographical coverage of state forests was not comprehensive, there were still gaps in the early records.

Changes in occupancy

To gain an understanding of the dynamic nature of the standard data set, we looked at the average percentage number of squares per region that changed occupancy from one year to the next for each region separately. Here we refer to any changes in occupancy from one year to the next such as R→N, B→G, G→N and so on (where R = red squirrel present, G = grey squirrel present, N = neither species recorded as present and B = both species present). Since the data were collected in a non-systematic way, we have used rank correlation to see if geographically adjacent regions showed similar trends in square occupancy. We also divided the data set up into two time periods, an early period from 1991/1992 to 1999/2000 when there were fewer records, and a later period from 2000/2001 to 2009/2010 when records were more numerous.

Trends in red squirrel occupancy

We plotted the proportion of squares occupied by red squirrels over the study period and, using simple linear regression, we looked for trends in the data and estimated when red squirrels would disappear (go extinct) in each region.

Results

The relationship between forest cover and the number of records

Overall, there were more red squirrel records than grey squirrels records across all forest cover classes (Fig. 4). Most squares (706) had no forest cover and yet the mean number of records per square was 4.4 grey squirrels and 7.3 red squirrels from the 20 years of data presented (Fig. 4). For this reason, we did not leave out squares without forest cover from our analyses. In general, there was an increase in the number of records with forest cover with one exception, that is a decline at 25-100% forest cover (Fig. 4). Overall, these data were likely influ-

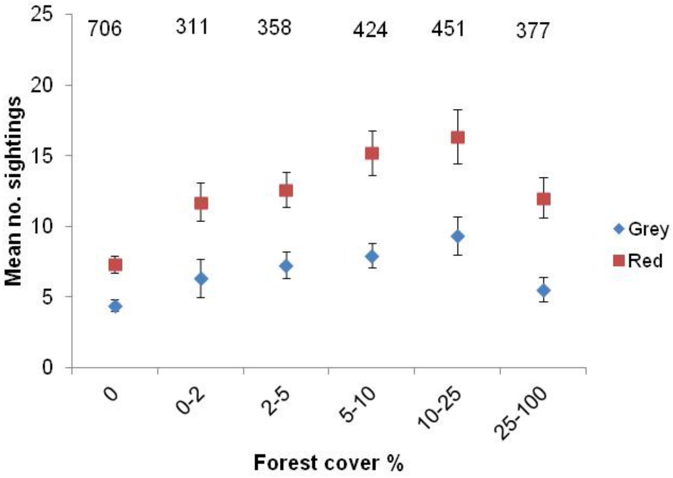

Figure 4 – The mean number of records (± standard error) of red and grey squirrels over the 20 year period according to forest cover. Numbers of squares in each forest cover class are shown at the top of the plot.

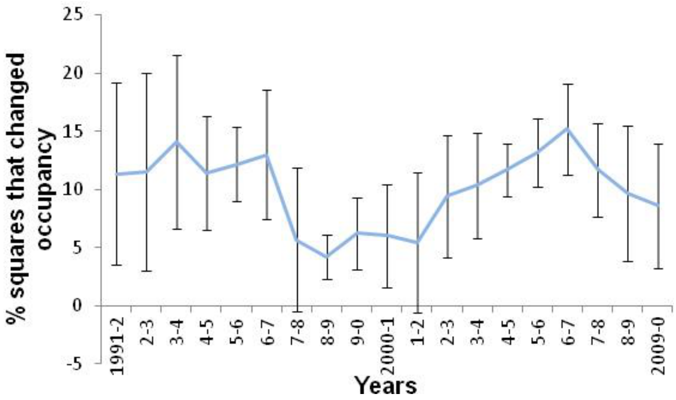

Figure 5 – The mean percentage number of squares which changed in reported occupancy from one year to the next throughout the study period with 95% confidence intervals.

enced by the distribution of people and, in the case of high forest cover, the ease of sighting a squirrel.

Changes in occupancy

The average percentage number of squares per region that changed occupancy from one year to the next varied between 4% and 15% but there was a considerable amount of variation among the regions (Fig. 5). The overall pattern was biphasic with less change in the period between 1997/8 and 2001/2. It also fell away towards the end of the study period (Fig. 5). The average percentage change in occupancy from 1996/7 to 2009/10 was 12% Northumberland (Coefficient of Variation 38%), 11% Cumbria (CV 52%), 10% South Scotland (CV 60%), 8% Central Lowlands East (CV 56%), 8% Central Lowlands West (CV 58%), and 8% North East Scotland (CV 59%).

Associations among the regional occupancy metrics were examined for the first nine transition years (period 1, 1991/1992 to 1999/2000) when there were fewer records, and the last 10 transition years (period 2, 2000/2001 to 2009/2010) when there were more records (Tab. 1). For the first period, there were only significant positive correlations between geographically adjacent regions in Scotland, between Central Lowlands West and Central Lowlands East, and Central Lowlands East and North East Scotland. For period 2, these associations were again found, and stronger, but there were also significant positive associations between South Scotland and Central Lowlands East, South Scotland, and Central Lowlands West and the nonadjacent Central Lowlands West and North East Scotland. Occupancy metrics for Cumbria and Northumberland were not associated with each other or with and Scottish regions in either period. It is to be expected that adjacent regions may show some similarity in changes in square occupancy and this can be seen for the Scottish regions, especially for period 2 with the larger data set. However, records for Cumbria and Northumberland were not associated with each other, or with the South of Scotland, indicating the importance of looking at the distributional data on a regional basis.

Table 1 – Spearman's rank correlation coefficient matrix among the changes in occupancy indices for the six different regions: above the cross diagonal for (a) 1991/2-1999/00 (N=9), and (b) 2000/01 to 2009/10 (N=10). ND = Northumberland, C = Cumbria, SS = South Scotland, CLW = Central Lowlands West, CLE = Central Lowlands East, NES = North East Scotland. Bold coefficients, p<0.05.

a) 1992/1992 to 1999/2000 (N=9)

Region	C	SS	CLW	CLE	NES
ND	0.256	0.077	-0.61	-0.443	-0.61
C		0.669	0.244	0.127	-0.361
SS			0.597	0.595	0.042
CLW				**0.770**	0.583
CLE					**0.753**

b) 2000/2001 to 20099/2010 (N=10)

Region	C	SS	CLW	CLE	NES
ND	0.185	-0.018	-0.015	0.025	0.015
C		0.08	0.074	0.272	-0.006
SS			**0.854**	**0.640**	0.480
CLW				**0.844**	**0.758**
CLE					**0.908**

Changes in red squirrel distribution

The rate of decline in red squirrel square occupancy differed across the regions with the exception of Central Lowlands East (Fig. 6). Here, red squirrel occupancy started in 1991 at a much lower level than the other regions and it declined in a rather shallow and erratic manner until the last three years where it increased considerably. However, in agreement with Central Lowlands East there was an upward turn in the last two or three years across all regions, especially for South Scotland where numbers appeared to be falling sharply until towards the end of the study period. With the exception of Central Lowlands East, the linear regression models provide reasonable fits to the data with high R^2 values for Northumberland, Cumbria, Central Lowlands West and North East Scotland, and moderate R^2 value for South Scotland (Tab. 2). Estimated extinction times are in the 2020s for Northumberland, Cumbria and Central Lowlands West, 2067 for South of Scotland and 2104 for North East Scotland.

Discussion

Squirrel records and changes in distribution

Tree squirrels should be amenable to distribution studies at the landscape scale because they are likely to occupy all tracts of woodland consisting of seed-producing trees and are of sufficient connected area to support one or more squirrels (see Verboom and van Apeldorn

Table 2 – Least square estimates of the slope for the relationship between the number of squares occupied by red squirrels and year for each region, together with F statistics (in bold are significant, p<0.05) for the regression models, R^2 values and predictions of when red squirrels may disappear.

Region	Slope	$F_{1,18}$	R^2	Predicted year to go extinct
Northumberland	-10.40	132.60	0.88	2025
Cumbria	-12.90	458.20	0.96	2023
South Scotland	-9.70	51.00	0.74	2067
CL East	-0.80	1.80	0.09	-
CL West	-9.40	473.70	0.96	2029
North-east Scotland	-2.10	137.70	0.88	2104

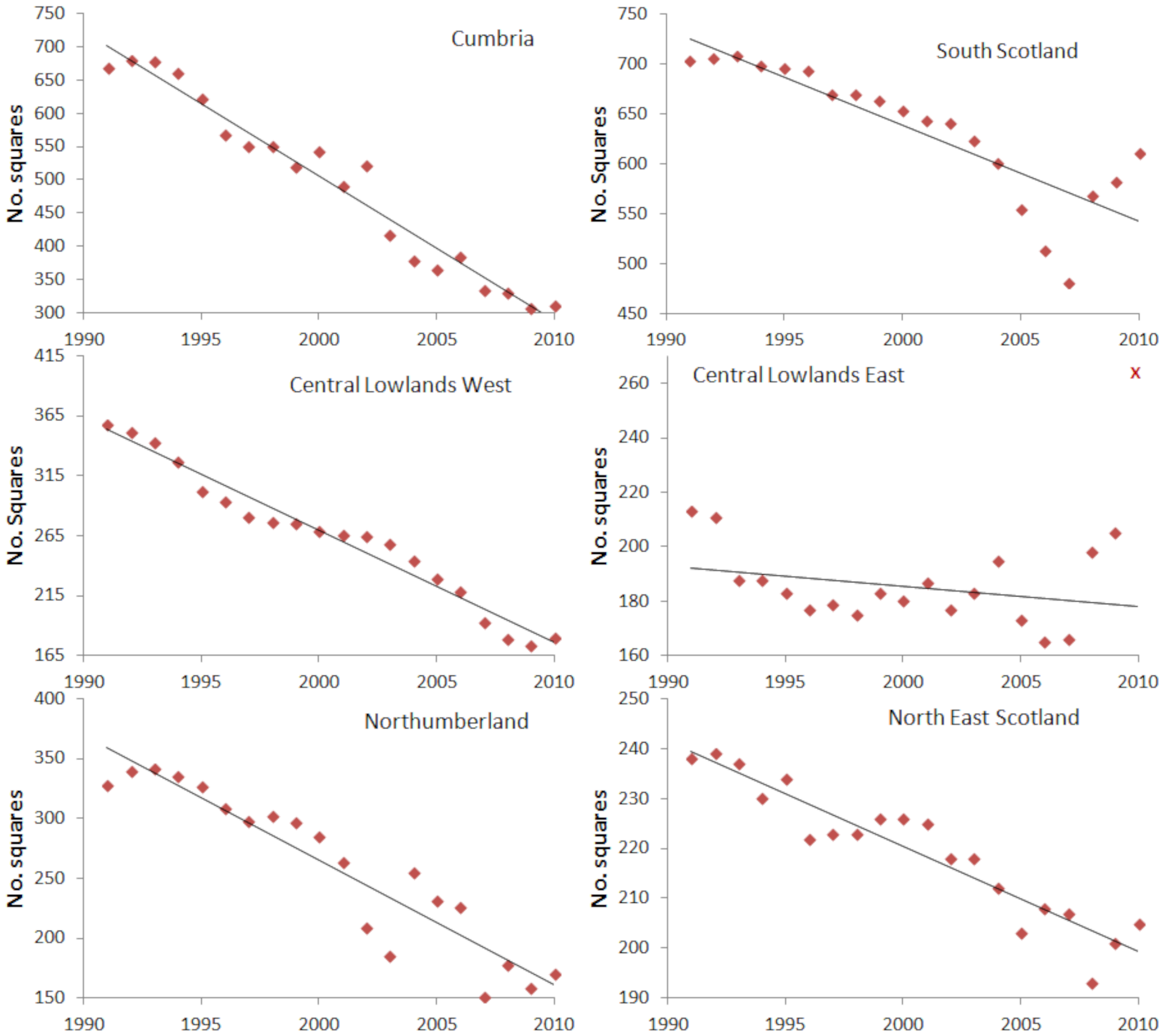

Figure 6 – Changes through time in the number of squares in each region occupied by red squirrels. The trend lines are fitted least square linear regression lines. In Central Lowlands East, point x was omitted from calculating the regression line.

1990; Andren and Delin 1994; Rodriguez and Andrén 1999; Delin and Andrén 1999; Gurnell et al. 2002; Verbeylen et al. 2003; Koprowski 2005). However, the results show that red and grey squirrels were often recorded in squares which had no tree cover as the dominant habitat according to the CORINE Land Use cover maps used. The smallest mapped unit in CORINE is 25 m^2 (http://www.eea.europa.eu/publications/COR0-landcover) and this spatial resolution of the land cover may not be sufficiently detailed to include tree rows, small woodlands or gardens where squirrels are often seen. The utility of records of squirrel presence made by the public could be improved if data were collected at high (i.e. nearest 10 or 100 meters) resolutions and linked to detailed land cover maps not available in this study. This would allow records to be linked with landscape structure information (e.g. dispersal links such as tree rows) as well as more detailed habitat information

The data set compiled between 1985 and 2010, of which only part has been explored in this paper, represents a considerable effort by volunteers and the organisations involved in receiving and holding data. The number of records has considerably improved over the years as the public became more engaged with the plight of the native red squirrel. Nevertheless, there has until now been no systematic analysis of the data to assess its utility and whether improvements to the recording scheme could be helpful.

The reported changes in occupancy indicate a great deal of flux occurring, with changes often bidirectional, that is changes occurring from red squirrel occupancy to grey squirrel occupancy and vice versa. This may partly result from natural processes affecting grey squirrel range expansion and contraction such as annual tree seed crop size (Gurnell, 1996; Andren and Lemnell, 1992), outbreaks of Squirrelpox virus (SQPV) carried by grey squirrels but fatal to red squirrels (e.g. Bruemmer et al. 2010), or the control of grey squirrels which has been increasing and more targeted over the last 4 or 5 years of the study period (e.g. see Parrot et al. 2009, 2010, also Scottish Natural Heritage 2010). However, there were insufficient data on any of these factors to carry out a detailed analysis. Understanding how management activities affect the rate of replacement of red by grey squirrels is a key question and requires the identification of control effort and return on that effort. Such control requires targeted squirrel monitoring at the local level before and after the control actions to assess effectiveness. Understanding how SQPV as well as grey squirrel control affect red squirrel conservation are recognised as challenges for the future squirrel management actions in the UK (Parrot et al., 2009, 2010). At present, it is speculation as to whether the apparent upturn in the fortunes of red squirrels within the last three or four years based on this study result from grey squirrel control. What is evident is that there were differences in the replacement of red by grey squirrels in the different regions. This is partly down to historical factors, such as the presence of grey squirrels in the Central Lowlands over a long period of time, but also to habitat composition (e.g. presence of deciduous woodland) and ease of dispersal of grey squirrels (presence of tree or hedgerow links across landscape matrix). Also, it has been suggested recently that the genetic diversity of grey squirrel populations influences their speed of spread (see Signorile et al. 2014). The decline in square occupancy throughout all regions except Central Lowlands East gives estimates of time to extinction, which seem reasonable but clearly could change in light of the factors discussed above. Looking at the trends in the data presented, red squirrels may disappear from the north of England and Central Lowlands West in the mid to late 2020s, but they would survive until 2067 in the South of Scotland and 2104 in North-east Scotland.

Effects of climate change

It is possible that climate change may have an influence on the distribution of red and grey squirrels in the future, but as yet not in predictable ways. Climate warming may directly impact on squirrel populations by, for example, improving overwinter survival (Gurnell, 1996), but it will also affect the seed masting and the future composition of woodlands (Shuttleworth et al., 2012). This in turn will affect squirrel survival and fecundity (Gurnell, 1996) as well as red-grey squirrel interactions and competition (Gurnell et al., 2004). Similarly, if seed crops increase in abundance and regularity, they are likely to affect grey squirrel expansion at the expense of red squirrels. Managers of state or private forests are also likely to adjust future plantings with trees that are more tolerant of warmer, drier conditions, and more resistant to tree diseases such as *Phytophthora*, and other threats such as wind and fire (Ray et al., 2010).

Volunteer surveys pre- and post 2010

The data explored in this paper have been collected in an unsystematic and uncoordinated manner by volunteers from across large geographic areas. Overall, numbers of records have increased steadily over the period 1991-2010 as conservation organisations have continued to raise awareness of the potential plight of the native red squirrel. These data reveal changes in the distribution of both species and produced plausible, yet crude estimates of extinction times for red squirrels within different regions of the north of England and Scotland. Nevertheless there has been a certain amount of data redundancy by limiting the analysis to one record of squirrel presence per year and there have been large numbers of gaps in the records for many squares across the period of the survey. Moreover, the data are too unstructured to use standard, more reliable models (e.g. occupancy analysis) to provide more robust estimations of extinction times or to monitor directly the effects of management actions. Admittedly, volunteer based public surveys over large geographic areas engage the public and have PR (public relations) value as well as providing data on distributions. However, to provide quality data, it is necessary that surveys have clearly defined aims, and are systematic, centrally coordinated, repeated at appropriate times and sufficiently resourced (MacKenzie and Royle, 2005; Crall et al., 2010).

Since the initial collation of squirrel distribution data for this research, and the work by Parrot et al. (2009, 2010) identifying a lack of systematic survey work on red and grey squirrel presence and abundance and information on management effort, squirrel monitoring and data collection has improved. Both the main Scottish and English squirrel projects now have systematic monitoring at different scales and central coordination (Brassey et al., 2013; Seward, 2013). For example, the Saving Scottish Red Squirrels Project has monitoring at a broad or national scale involving sightings data from the public; regional-scale, systematic surveys based on feeder box monitoring or visual transects in selected sites to determine squirrel species presence; and fine-scale, local data on specifically chosen woodlands to monitor population trends (Brassey et al., 2013). These data, combined with detailed record keeping on grey squirrel control efforts (White and Lurz, 2014) should allow expanded, statistical analyses on the collected sightings data, such as occupancy modelling (e.g. see MacKenzie and Royle 2005; Mortelliti and Boitani 2008) and more robust population trends (e.g. White and Lurz 2014). Hopefully, these improved and systematic surveys with the assistance of volunteers will provide detailed information on how management actions are benefitting the conservation of red squirrels.

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