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How have recent lepidopteral colonisers fared in Yorkshire?

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Introduction

Yorkshire's latitude places it at the northern edge of the ranges of several butterfly species whose populations have waxed and waned over the last two centuries for which we have sufficient extant records. Since the 1990s butterflies once considered rare or absent in Yorkshire, such as Comma *Polygonia c-album*, Speckled Wood *Pararge aegeria*, Gatekeeper *Pyronia tithonus* and Holly Blue *Celastrina argiolus* have expanded northwards to become commonplace (Asher *et al*., 2001; Fox *et al*., 2007). There has even been the arrival of Essex Skipper *Thymelicus lineola*, a butterfly whose northern range has historically always been to the south of Yorkshire. It is not always clear what mechanisms drive expansion and restriction in range but clearly sustained increases in global mean temperature from the early twentieth century onwards (Stott *et al.*, 2000; IPCC, 2013) has been a major factor (Asher *et al., loc. cit.*; Parmesan *et al*., 1999). This article aims to review how the Speckled Wood, Comma, Gatekeeper, Holly Blue and Essex Skipper have fared in Yorkshire by comparing the status of these butterflies in the period

2004-2017 against the previous period of 1995-2003. The analysis will provide an update to Frost (2005) on how these recent lepidopteral colonisers of Yorkshire have fared.

Past status

Speckled Wood. Subject to large changes in range; a notable retraction from around the 1860s to the 1920s left Speckled Wood confined to the south-west of England, Wiltshire and parts of Dorset and West Sussex, lowland Wales and western Scotland (Asher *et al*., *loc. cit.*; Thomas & Lewington, 2014). Common in Yorkshire around the 1850s (Morris, 1853; Porritt, 1883), Speckled Wood was largely lost to Yorkshire by the end of the nineteenth century, with only one site (Wentbridge) still producing records to the 1970s. The first modern northwards expansion into Yorkshire began in the 1990s (see Frost, 2005).

Gatekeeper. Widely distributed and abundant in southern England, but with a habit of experiencing periodic expansions and contractions in distribution (Asher *et al*., *loc. cit.*; Thomas & Lewington, *loc. cit.*). Extant records suggest it was not particularly widespread in Yorkshire from the 1830s onward; Porritt (*loc. cit.*) suggests stronger presence along the east coast as far north as Whitby falling off towards the interior. There was a contraction back to the southern edge of Yorkshire by the late 1800s (see Frost, *loc. cit*). It remained a scarce butterfly in Yorkshire until the 1980s when there was evidence of movement into the Sheffield area (Whiteley, 1992).

***Comma*.** Common throughout England and Wales now, but suffered a collapse in numbers in the early nineteenth century that left it largely confined to the Welsh borders by the end of the century (Asher *et al*., *loc. cit.*; Thomas & Lewington, *loc. cit.*). It was virtually absent from southern England for almost a hundred years between 1830 and 1930. Numbers started to build in the south around 1910-20, with the beginnings of a northwards expansion into Yorkshire marked by sporadic sightings in VC61 and VC63 in the 1940s. The first true expansion into Yorkshire was noted in the early 1980s (see Frost, *loc. cit.*).

***Holly Blue*.** Though it declined nationally in the nineteenth century, the Holly Blue has suffered less than many of Britain's other butterflies during the last hundred years and has enjoyed gentle expansion in the last thirty years or so (Asher *et al*., *loc. cit.*; Thomas & Lewington, *loc. cit.*). Though a colony was present in York, Harrogate and Nidderdale from 1978, the first general expansion into Yorkshire came from the south in 1990. Large numbers were reported in VC61 and large swarms came in from the east at Spurn, presumably as northwards movement shearing back into land (Frost & Frost, 1991; Frost, *loc. cit.*).

***Essex Skipper*.** This is a butterfly new to Yorkshire in 1996 when it was seen at Wintersett Reservoir near Wakefield in VC63. It has since expanded locally in areas around Doncaster. A separate point of entry into Yorkshire was effected presumably by passage across the Humber estuary when a colony was established at Spurn NNR in 2003 (Frost, *loc. cit.*). After apparently stalling for around a decade, Essex Skipper has recently shown signs of renewed further expansion (Smith, 2015; Beaumont *et al*., 2016, 2017, 2018).

Method

The Butterfly Conservation Yorkshire (BCY) database was searched for records of the target butterflies for the period 1995 to 2017 from the five Watsonian vice-counties (VC61-VC65) traditionally comprising the county of Yorkshire for recording purposes.

Several measures were derived of the extracted records from the BCY database. *Levana* mapping software (version 3.98) allowed the easy creation of maps at tetrad resolution (2 x 2km squares) and also provided tetrad counts within those maps. To perform basic statistical tests SPSS 24 was used; to visualise data as density maps, calculate boundary lines and calculate surface areas, the *R* statistical package (*R* version 3.4.4, R Core Team, 2018) and additional statistical mapping packages were used (Calenge, 2006; Wickham, 2009; Kahle & Wickham, 2013; Baddeley *et al*., 2015; Becker *et al*., 2016; Becker *et al*., 2017; Schnute *et al*., 2017). The excellent *R* manual (Thomas *et al*., 2015) is highly recommended and helped in first motivating some of these spatial analyses.

Reference to butterfly range in this article includes the notion of National Character Areas (NCAs). These are useful entities defined by Natural England (2014) to capture distinctive natural areas of England that, due to a unique combination of landscape, bio- and geo-diversity, history and cultural and economic activity, can be seen as providing a meaningful 'sense of place'. The Yorkshire and Humber region spans 28 of these areas – as can be seen in the figure below this region follows natural topography rather than administrative boundaries, but nevertheless shows reasonable affinity to the five Watsonian vice-counties.

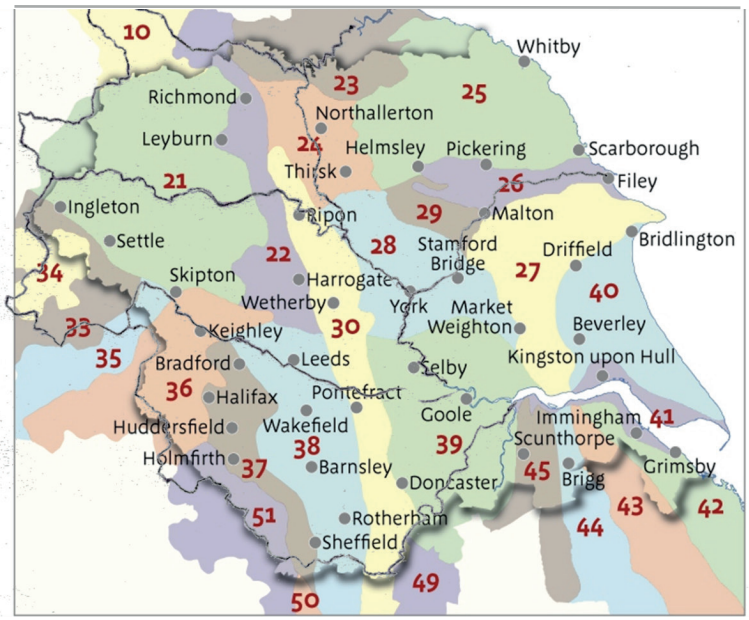

Figure 1. The Yorkshire and Humber region (delineated by the shaded boundary) comprises some 28 National Character Areas (NCAs) which are natural subdivisions of England (Natural England, 2014). The five Yorkshire VCs (61-65) boundary lines are shown superimposed upon the NCAs. The following numbering and names are those used by Natural England. The map contains public sector information licensed under the Open Government Licence v3.0.

NCA	NCA Name	NCA	NCA Name
10	North Pennines	36	Southern Pennines
21	Yorkshire Dales	37	Yorkshire Southern Pennine Fringe
22	Pennine Dales Fringe	38	Nottinghamshire, Derbyshire and Yorkshire Coalfield
23	Tees Lowlands	39	Humberhead Levels
24	Vale of Mowbray	40	Holderness
25	North Yorkshire Moors and Cleveland Hills	41	Humber Estuary
26	Vale of Pickering	42	Lincolnshire Coast and Marshes
27	Yorkshire Wolds	43	Lincolnshire Wolds
28	Vale of York	44	Central Lincolnshire Vale
29	Howardian Hills	45	Northern Lincolnshire Edge with Coversands
30	Southern Magnesian Limestone	49	Sherwood
33	Bowland Fringe and Pendle Hill	50	Derbyshire Peak Fringe and Lower Derwent
34	Bowland Fells	51	Dark Peak
35	Lancashire Valleys		

Results

***Speckled Wood*.** Figure 2 (p112) shows the tetrad distribution maps for Speckled Wood for the 1995-2003 period (Frost, *loc. cit.*), the current survey period 2004-2017 and the gains and losses between the two periods. It is important to underline that the following descriptions are based on the *cumulative* records for each time period; the dynamic year-by-year expansions and contractions are not captured. Nevertheless, it is arguable that long-term change in distribution is something that is best captured by a long exposure time rather than a short snapshot. The contour lines (in Figure 2: Top-left and Top-right) are drawn by eye and delineate which parts of Yorkshire have 'strong' presence of Speckled Wood (black bold contour line) and which areas are in the process of 'apparent' colonisation (black faint contour line).

In the period 1995-2003 Speckled Wood had a strong presence in the eastern half of VC63 expanding from the Southern Magnesian Limestone ridge, westwards into the Yorkshire Coalfield east of the Pennines and eastwards into the western half of the Humberhead Levels (Figure 2: Top-left). A band of partial colonisation some 20-30km wide surrounds the main area and extends to the east coast across the Holderness plain and the northern banks of the Humber Estuary. By 2017 (Figure 2: Top-right) the areas of partial colonisation in 1995-2003 have been fully colonised, with further dense colonisation into the Vale of York and the Vale of Mowbray, and the whole of the east coast extending some 10-20km inland is also heavily colonised from Bridlington up to the northern edge of VC62. The only areas of Yorkshire still only partially colonised are the Vale of Pickering, the Wolds, the Howardian Hills, the southern half of the North Yorkshire Moors and Cleveland Hills, the northern half of Holderness, and western VC64 (Yorkshire Dales). Speckled Wood is absent from the far north-west of VC65 (but this is an under-recorded area). Figure 2: Bottom-left shows the gains in tetrads from both 'filling in' known strong areas of colonisation in 1995-2003 but also the spectacular further spread of Speckled Wood over large areas of Yorkshire between the two survey periods (1995-2003 and 2004-2017). Figure 2: Bottom-right shows that there have been very few losses in

tetrads between the two survey periods.

Drawing lines by eye can be subjective (though as a pattern matcher the eye and brain is still unparalleled; witness the success of such citizen science endeavours as the exoplanet categorisation project which classifies transit light curve data from NASA's Kepler Space telescope to uncover planets orbiting other stars - see https://www.planethunters.org/.) However, calculation is more tricky for the eye! To characterise the areas of colonisation, the Speckled Wood reports for the period 1995-2003 – the Frost (*loc. cit.*) survey period – were turned into a density map. Figure 3: Left shows a density map overlaid over a satellite map of Yorkshire where the presence and number of reports at any location is taken into account (we are interested in both where butterflies have been spotted but also how many times they have been spotted there). Imagine water dripping onto a blotting pad so that individual water drops falling at a particular location make that spot increasingly damp. Further imagine that the dampness spreads in the blotting pad so that we have a smeared damp patch. Here we have instead of water droplets butterfly reports. What the density maps show is the evidence for the presence of a butterfly of a particular species (in this case Speckled Wood) in a location based on the recorded presence of the butterfly in *that location* plus the *surrounding regions*[1]. Each separate Speckled Wood report is represented by a yellow spot – the spots are semi-transparent so that repeated reports at one location build incrementally to increase yellow spot opacity. The white contour lines are different report densities so that increasingly packed contour lines indicate steeper gradients of report density (using the same logic as altitude contour lines in OS maps or barometric pressure isobars in weather maps). It is important to note that the contour lines are normalised to the records *within* the survey period so that they characterise the *relative* rather than *absolute* strength and distribution of records. As such they provide a nuanced picture of density within the survey period. To a certain extent highest report densities are over major urban centres – lots of people, lots of reports. The two most densely reported areas are Doncaster (especially south Doncaster) and the Wakefield, Barnsley and Pontefract areas. It is probably more instructive to look at the outermost contour line as it encloses a region where Speckled Wood is present even outside areas of major populations. It is clear that the density map (Figure 3: Left) captures rather neatly the patterns drawn by eye (Figure 2: Top-left) for 'strong' presence of Speckled Wood.

To *quantify* 'strong' presence within the density map, use was again made of kernels which are particularly well suited to bounding irregular distributions, to create 'habitat' maps (Calenge, 2006). A habitat map is the area of the *minimum* range in which there was a specified probability of encountering a butterfly. The advantage of such a notion is that a calculation can be made of the surface area in km^2 of the habitat map. To capture the region of 'strong' presence of a butterfly (equivalent to the bold contour line in Figure 2: Top-left and the outermost contour line in Figure 3: Left), the probability level of encountering a butterfly was set at 90% probability

1 Technically the method used is kernel density estimates. Each butterfly report produces a Gaussian distribution of probability centred at the location it was seen (think of a 3D bump at that location where we have the two dimensions of space x and y (longitude and latitude) and the third dimension of height z (denoting degree of presence). Each report adds one to the presence at that location). Finally, we sum up all the activations across the sampling grid spatially and in the z-dimension which means we produce a bumpy 3D map of presence which, if viewed from directly above the map, becomes a 2D density map. It is a 2D probability density distribution.

(denoted *strong-90*). The surface area of the *strong-90* region for the survey period 1995-2003 is 3,420km^2. To quantify 'apparent' colonisation the specified probability was relaxed to 99% chance of encountering a butterfly, denoted the *weak-99* region. This region effectively spans all of Yorkshire where there has been some evidence of a Speckled Wood being seen. The surface area of the filled *weak-99* region for the survey period 1995-2003 is 10,009km^2, which after the subtraction of the *strong-90* region, means that the *weak-99* area covers 6,589km^2. Figure Appendix 1: Top (first) row shows these 'habitat' maps calculated for Speckled Wood where the habitat region is filled white. Comparison between Figures 2, 3 and Figure Appendix 1 maps show a fairly close agreement between patterns revealed in all figures.

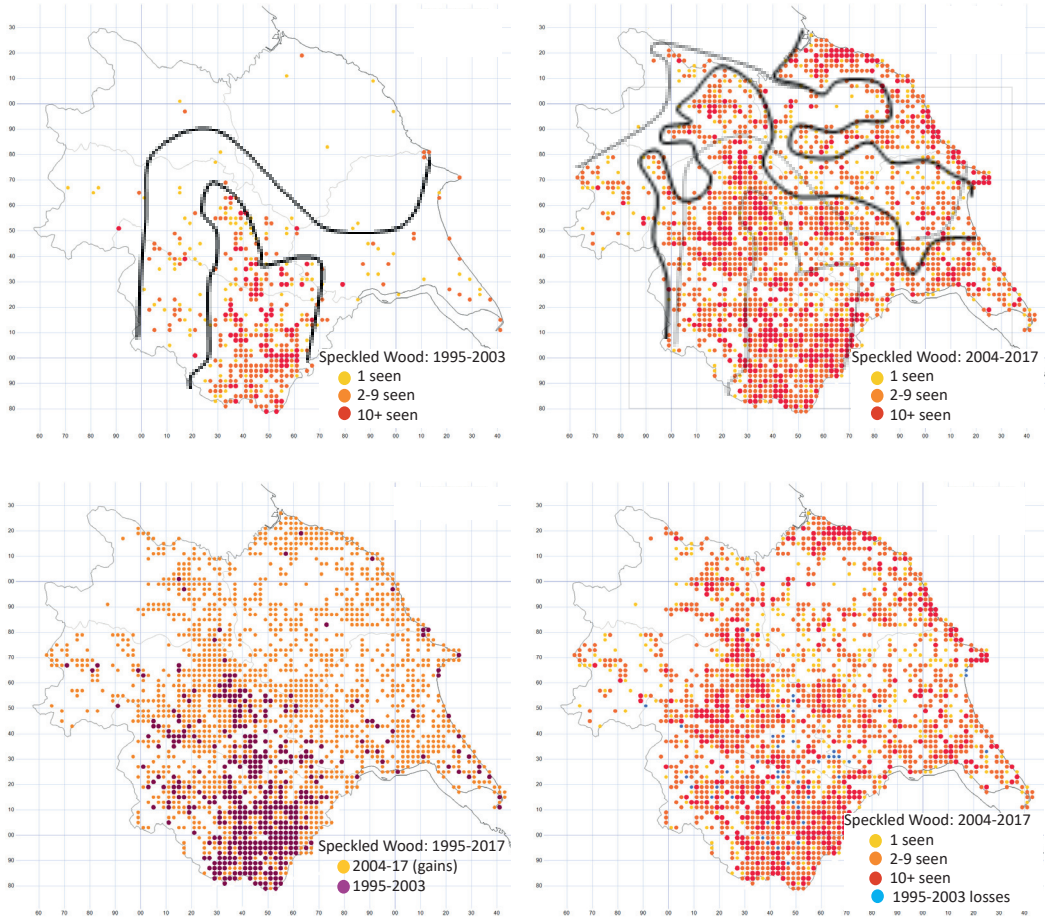

Figure 2. Levana tetrad distribution maps for Speckled Wood *Pararge aegeria*. Top-left: 1995-2003: The survey period reported in Frost (2005). Speckled Wood present in 430 of 3232 recorded tetrads (=13.3%). The black bold contour line marks 'strong' presence and the black faint contour line marks 'weak' presence, suggestive of colonisation. All contour lines drawn by eye. Top-right: 2004-2017. Speckled Wood present in 2023 of 3720 recorded tetrads (=54.3%). The black bold and faint contour lines same meaning as in Top-left. The 1995-2003 contour lines have been redrawn but in grey. Bottom-left: Comparison between the two periods with gains shown as orange dots. Bottom-right: Comparison between 1995-2003 and 2004-2017 with losses shown as blue dots.

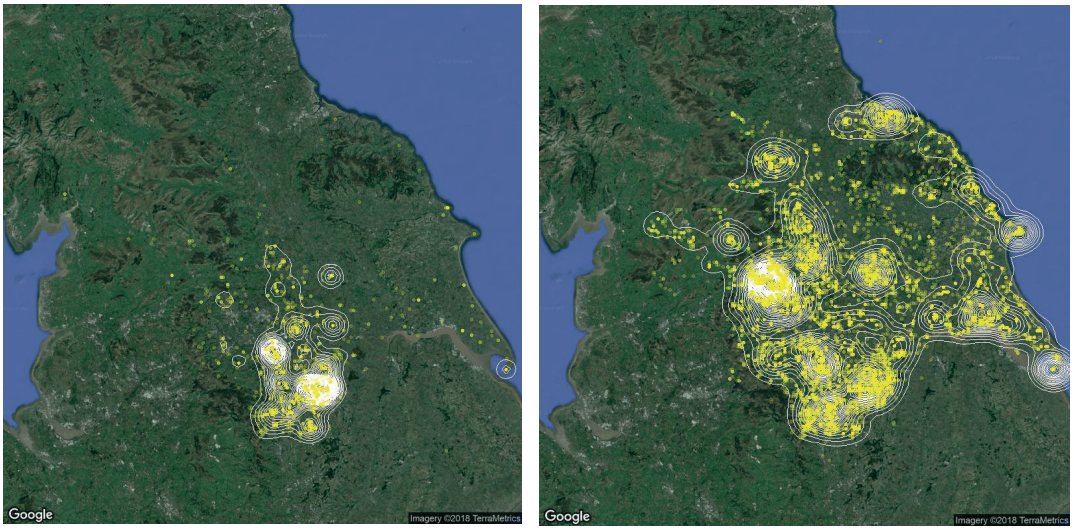

Figure 3. Speckled Wood density maps overlaid over Yorkshire for the survey period 1995-2003 (left) and 2004-2017 (right). Individual reports of Speckled Wood are shown as semi-transparent yellow dots, with multiple reports at the same location being overlaid on top of each other thus determining dot opacity. The density maps represent the probability distribution across Yorkshire of the presence of Speckled Wood. They can be thought of loosely as representing the evidence of the presence of Speckled Wood in any one location based on the recorded presence and abundance of the butterfly in *that location* plus the *surrounding regions*. The white contour lines delineate zones of increasing density normalised to the range within the individual survey periods.

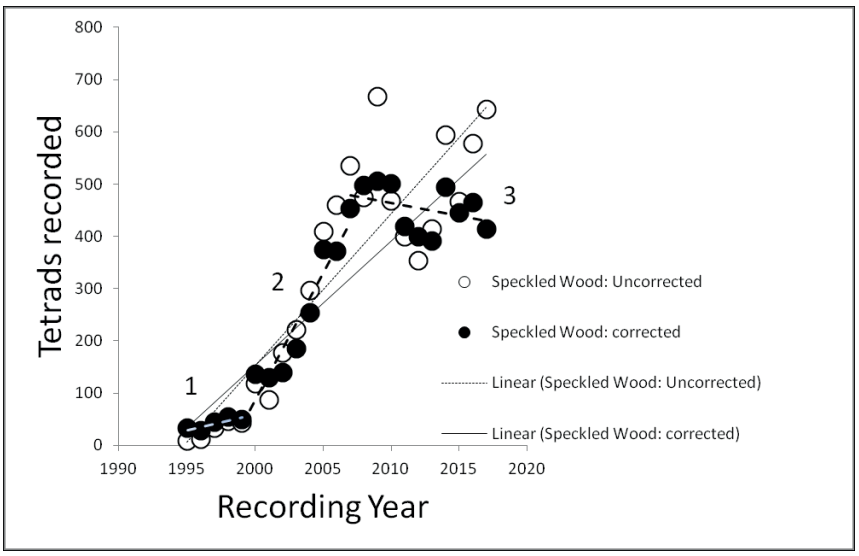

Figure 4. Number of tetrads in Yorkshire where Speckled Wood was seen as a function of recording year. Three distinct phases can be discerned: negligible growth (1995-1999), rapid growth (1999-2007), and then stability (possible decline) between 2007-2017 (marked respectively 1, 2 and 3).

The same method as above was used to create density maps for the Speckled Wood reports for the survey period 2004-2017. Figure 3: Right shows in the most recent survey period of 2004-2017 that Speckled Wood report numbers have greatly increased (compare the number of yellow dots!), that there has been a spread throughout Yorkshire, and that the focus of greatest reports has shifted to Leeds. The story that the density map shows is consistent with the description given above for Figure 2: Top-right.

The *strong-90* and *weak-99* regions were also calculated for the Speckled Wood 2004-2017 reports using the same kernel boundary methods and criteria as outlined above to create habitat maps, see Figure Appendix 1: Bottom row. The habitat map surface areas calculated were 11,607km^2 and 13,634km^2 for the *strong-90* and *weak-99* regions respectively. The area in km^2 of the strong presence of Speckled Wood in Yorkshire has grown by a factor of 3.4 and the area in km^2 of apparent presence of Speckled Wood in Yorkshire has grown by a factor[2] of 2.07. We can see that the area of apparent colonisation in 1995-2003 has been fully colonised by 2004-2017 (compare Figure 2: Top-left faint black line with Figure 3: Right).

Figure 4 plots the number of tetrads in Yorkshire where Speckled Wood was seen during each recording year. The open circles represent number of tetrads with no correction for the number of tetrads recorded in the recording year. Given there is a correlation with recorder effort and number of tetrads returned, it is wise to attempt to correct for this. Please see Figure Appendix 2 for Levana maps showing number of visits for the periods 1995-2003 and 1995-2017. It is clear that increased recorder effort is reflected in a much greater number of tetrads visited and visited multiple times. To attempt to ameliorate this bias, the number of tetrads with Speckled Wood returned in each year was multiplied by a correction factor calculated as the number of tetrads recorded in that year divided into the mean number of tetrads for all years between 1995 and 2017.

Thus in 1995 there were 9 tetrads with Speckled Wood reported from a total of 334 tetrads recorded in that year for all butterflies, which when corrected becomes $9*(x/334) \rightarrow 33$ where x is the mean number of tetrads recorded between 1995 and 2017 and is equal to 1218. Similarly in 2017 there were 644 tetrads with Speckled Wood reported from 1889 tetrads recorded in that year for all species, which when corrected becomes $644*(x/1889) \rightarrow 415$.

A note of caution is due here as the correction factor x represents an average measure of recorder effort and will work more or less for any one particular butterfly species as far as the recorder effort for that butterfly species is typical of the average recorder effort *for all* Yorkshire butterfly species. However, the five target butterfly species reviewed here are common in Yorkshire so we can with some confidence assume that recording effort for each of them closely matches the average recorder effort for all butterflies. The solid circles represent number of tetrads with a correction for the number of tetrads in a given recording year. The dotted line is the best-fit linear regression where there has been no correction in number of tetrads recorded from within a given year and the solid line is where there has been a correction applied to

2 Factor comparisons are probably wiser than absolute numbers comparisons (in km^2) because any 'errors' in drawing the density and habitat maps will tend to cancel out. For instance, the habitat maps (Appendix Figure 1) include areas of the sea or neighbouring VCs which contribute to the km^2 number but will fall out in a factor comparison.

the number of tetrads recorded from within a given year. Tetrads recorded (corrected) is significantly related to recording year (bivariate Pearson correlation, two-tailed $r(23) = 0.894$, 95% CI [0.805, 0.953], $p < 0.001$). There has been a 5.7 fold increase in the number of tetrads occupied by Speckled Wood between 1995 (n=33) and 2017 (n=415) when tetrad number is controlled for the increase in recording[3]. Further inspection of Figure 4 suggests that the rise in the number of tetrads with Speckled Wood records as a function of recording year can be broken down into three distinct phases: negligible growth (1995-1999), rapid growth (1999-2007), and then stability (possible decline) between 2007-2017 (marked respectively 1, 2 and 3 in Figure 4).

Gatekeeper (Fig.6 p116)**.** Figure 5 shows the tetrad distribution maps for Gatekeeper for the 1995-2003 period (Frost, *loc. cit.*), for the period 2004-2017 and the comparison between the two periods. Gatekeeper had a strong presence in the south and south-east of Yorkshire by 1995-2003 (Figure 5: Top-left). There was a northerly zone of partial colonisation reaching to about Scarborough (40km northwards from Hornsea at the most easterly point) and reducing to 15-20km wide at the most westerly point in the acidic gritstone moorlands west of the Vale of York. There was also a narrower range of eastwards colonisation (about 15-20km wide) running through VC63 and VC64, with a further 20km westwards tongue of colonisation to Settle about 10km wide in the lower Yorkshire Dales. By 2004-2017 (Figure 5: Top-right) the areas where Gatekeeper had a strong presence in 1995-2003 have been further filled in. The northerly expansion has largely failed to materialise and there has been a marginal shift of 15-20km west reducing northwards, with further movement into the Vale of York. The main expansion has been in the areas of partial colonisation which have expanded into the northernmost parts of VC62 and north east into the south east of VC65. The lack of significant northwards expansion on the eastern side of Yorkshire is presumably due to the higher inland altitudes of the North York Moors. Figure 5: Bottom-left shows that gains have been largely restricted to the filling in of tetrads in the strong presence areas of 1995-2003. Figure 5: Bottom-right shows that losses have been largely restricted to VC61 and VC62.

Density maps for Gatekeeper records for the survey periods 1995-2003 and 2004-2017 are shown in Figure 7. Again there is an encouraging match in patterns between boundary lines drawn by eye (Figure 5, p116) and calculated density maps (Figure 7, p117). The 2004-2017 density map hints that the relative strength of Gatekeeper has shifted towards the western parts of Yorkshire (particularly Leeds) with some fall off in spread density in the Holderness plain. The *strong-90* and *weak-99* habitat region surface areas were calculated for Gatekeeper for the survey periods 1995-2003 and 2004-2017 reports using the same kernel boundary methods and criteria as used for Speckled Wood (for the sake of brevity these maps have been omitted). The habitat surface areas calculated were 8,313km^2 and 6,271km^2 for the *strong-90* and *weak-99* regions respectively for Gatekeeper in 1995-2003. For Gatekeeper 2004-2017, the habitat surface areas calculated were 7,875km^2 and 6,224km^2 for the *strong-90* and *weak-*

3 If we do not correct for growth in recording activity across the years then there has been a 72-fold increase between 1995 (when there were 9 Speckled Wood tetrads) and 2017 (when there were 644 Speckled Wood tetrads). That would be a biased comparison because there was relatively little recording going on in 1995 (coupled with few Speckled Woods) which underlines the need for a correction factor when comparing numbers across the years to avoid confounding the two variables of report activity and butterfly presence.

99 regions respectively. These numbers support the observations by eye that the range of Gatekeeper does not appear to have increased since 1995-2003 (and even hints at retraction) in some areas (Figure 5: Bottom-right, Figure 7: Right).

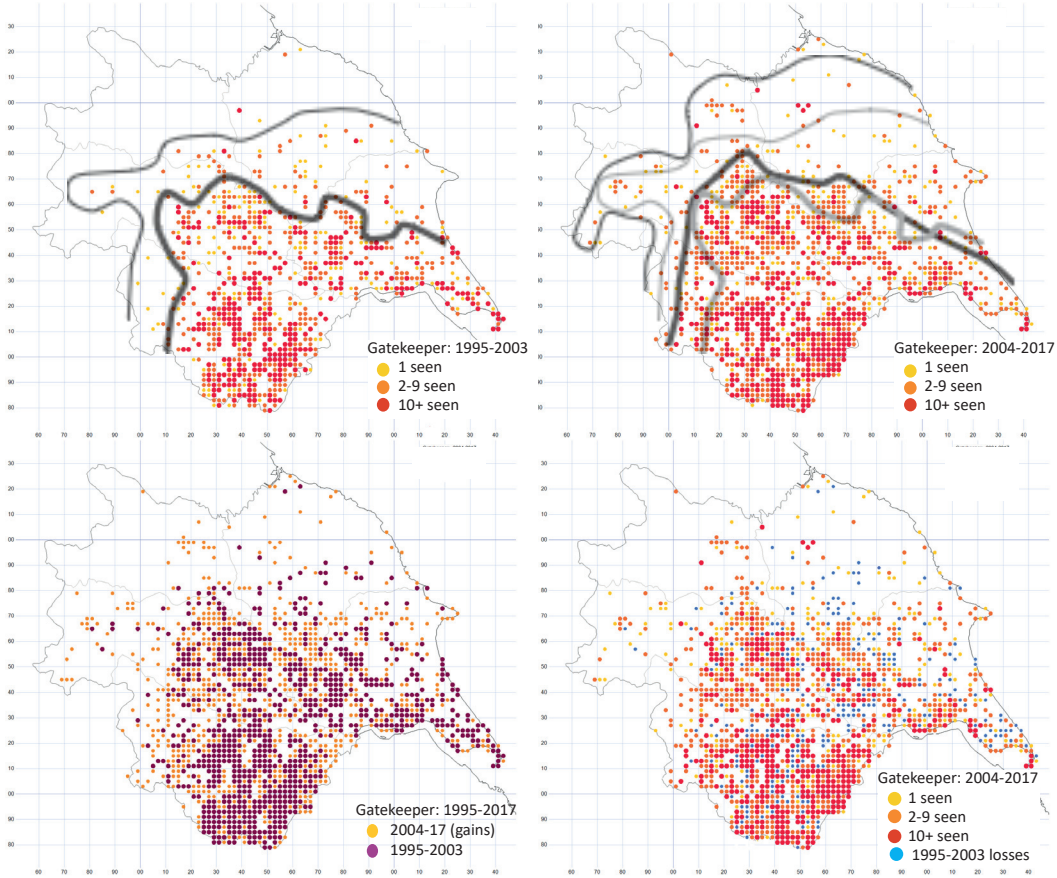

Figure 5. Tetrad distribution maps for Gatekeeper *Pyronia tithonus*. Top-left: 1995-2003. The survey period reported in Frost (2005). Gatekeeper present in 826 of 3232 recorded tetrads (=25.5%). Top-right: 2004-2017. Gatekeeper present in 1280 of 3720 recorded tetrads (=34.4%). Comparison between 1995-2003 and 2004-2017 with gains (Bottom-left) and losses (Bottom-right). Please see Figure 2 for further details.

Figure 6.
Left: Male Gatekeeper *Pyronia tithonus*
Right: Comma *Polygonia c-album*

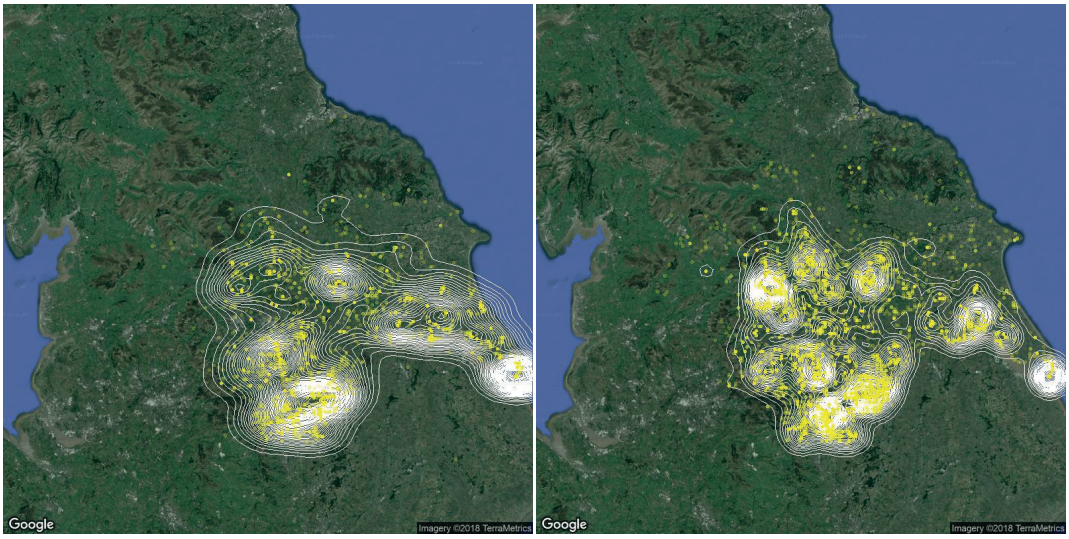

Figure 7. Gatekeeper density maps overlaid over Yorkshire for the survey period 1995-2003 (left) and 2004-2017 (right). For explanation of maps please see Figure 3.

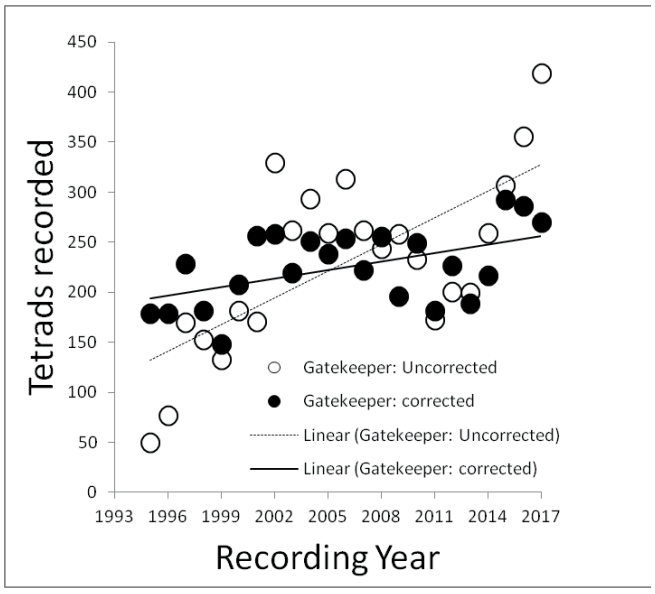

Figure 8. Number of tetrads in Yorkshire where Gatekeeper was seen as a function of recording year.

Figure 8 plots the number of tetrads in Yorkshire where Gatekeeper was seen as a function of recording year. The solid line is the best-fit linear regression where there has been a correction applied to the number of tetrads recorded from within a given year. Tetrads recorded (corrected) is significantly related to recording year ($r(23) = 0.498$, 95% CI [0.095, 0.769], $p = 0.016$). There has been a 30% increase in tetrad coverage between the two survey periods of 1995-2003 and 2004-2017, but this has largely been due to filling in of already colonised areas (Figs. 5 & 7).

Comma (Fig. 6 p116). Figure 11 (p120) shows the tetrad distribution maps for Comma for the 1995-2003 period (Frost, *loc. cit.*), for the period 2004-2017 and the comparison between the two periods. By 1995-2003 there was a strong presence in three areas in Yorkshire (Figure 11: Top-left). The largest area of concentration was the Southern Magnesian Limestone ridge, extending westwards into the Yorkshire Coalfield, the Southern Yorkshire Pennine Fringe and the Pennine Dales Fringe. This roughly rectangular area of land measures about 40km wide by 100km high. There was a second area of high concentration occupying the south east of Yorkshire (most of VC61) covering the Wolds and the Holderness plain, extending into the Vale of York. These two larger areas of dense colonization are separated by the Humberhead Levels. There was a smaller area comprising the woods of the lower slopes of the North York Moors. The areas of partial colonisation extended across the rest of Yorkshire excepting perhaps the outermost fringes of VC64 and VC65. However, these areas are notoriously under-recorded. By 2004-2017 (Figure 11: Top-right) the two largest areas of strong presence have merged as the Humberhead Levels were colonised leaving the Comma present across the entire south and south east of Yorkshire. The concentration in the North York Moors is largely the same but two new areas of strong presence have appeared; the first in the Middlesbrough area (in the Tees Lowlands) and the second around Richmond and Leyburn (Pennine Dales Fringe) and parts of the Vale of Mowbray. Inspection of the gains and losses between 2004-2017 and 1995-2003 (Figure 11: Bottom row) shows more gains than losses, with no particular discernible pattern.

Density maps for Comma records for the survey periods 1995-2003 and 2004-2017 are shown in Figure 9. Once again there is a welcome match in patterns between boundary lines drawn by eye (Figure 11) and the computer-generated density maps (Figure 9). The 2004-2017 density map hints that the relative strength of Comma has retracted somewhat in upper VC61 and the lower half of VC62, with greater densities achieved in western Yorkshire especially along the Southern Magnesian Limestone ridge. However, it should be noted that there are a *lot more* records in the second period as shown by the much greater number of white dots, each mapping a Comma report. The surface areas calculated were 12,682km^2 and 8,236km^2 for the *strong-90* and *weak-99* habitat regions respectively for Comma in 1995-2003. For Comma 2004-2017, the surface areas calculated were 11,077km^2 and 8,436km^2 for the *strong-90* and *weak-99* regions respectively. There has been a slight retraction in the strong presence areas.

Figure 10 plots the number of tetrads in Yorkshire where Comma was seen as a function of recording year. The solid line is the best-fit linear regression where there has been a correction applied to the number of tetrads recorded from within a given year. Tetrads recorded (corrected) is significantly related to recording year ($r(23) = 0.574$, 95% CI [0.153, 0.783], $p = 0.004$). There has been a 45% increase in tetrad coverage between the two survey periods of 1995-2003 and 2004-2017, which is largely due to filling in within strong presence areas along the Southern Magnesian Limestone ridge (Figure 11: Bottom-left). Gains in tetrads in the eastern half of Yorkshire (northern VC61 and southern VC62) are largely balanced out by losses.

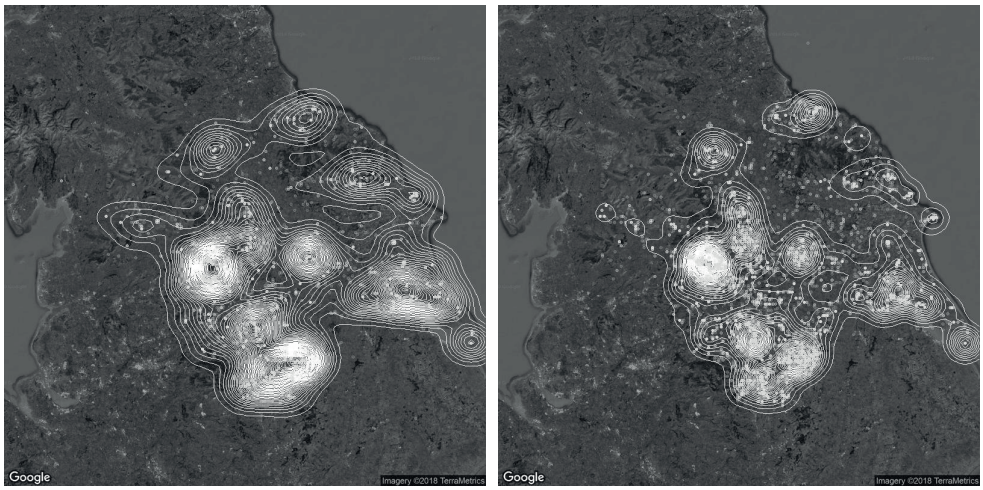

Figure 9. Comma density maps overlaid over Yorkshire for the survey period 1995-2003 (left) and 2004-2017 (right). For explanation of maps please see Figure 3.

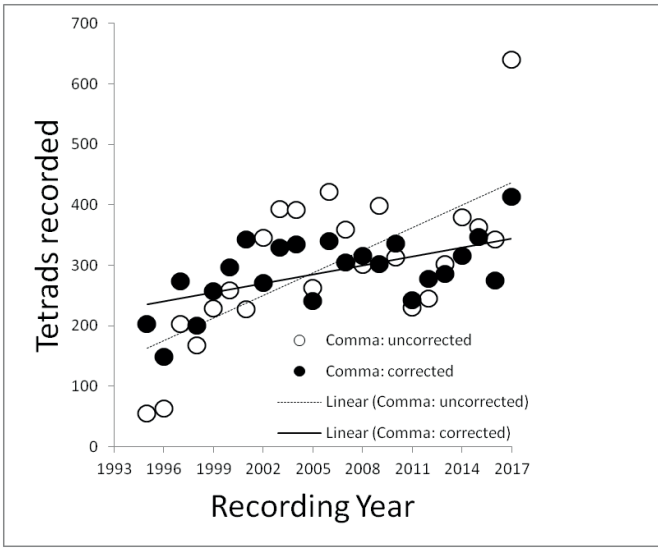

Figure 10. Number of tetrads in Yorkshire where Comma was seen as a function of recording year.

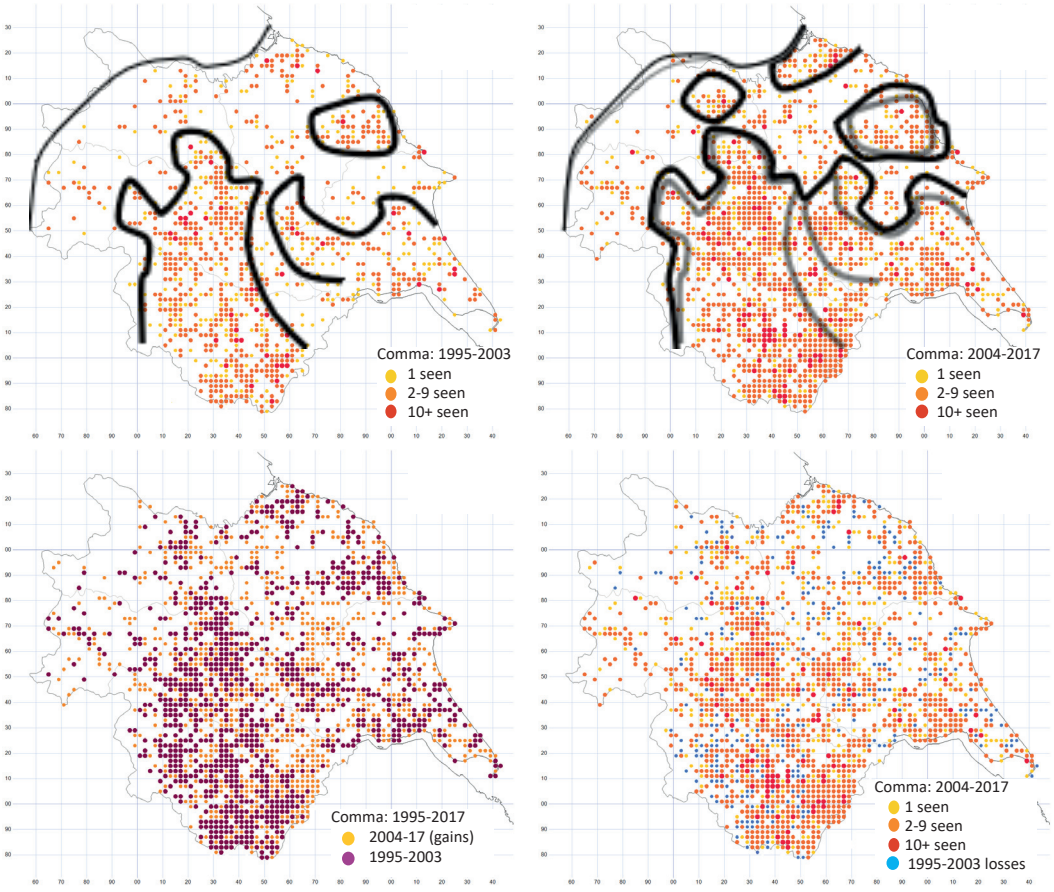

Figure 11. Tetrad distribution maps for Comma *Polygonia c-album.* Top-left: 1995-2003. The survey period reported in Frost (2005). Comma present in 998 of 3232 recorded tetrads (=30.8%). Top-right: 2004-2017. Comma present in 1927 of 3720 recorded tetrads (=51.8%). Comparison between 1995-2003 and 2004-2017 with gains (Bottom-left) and losses (Bottom-right). Please see Figure 2 for further details.

Holly Blue (Fig.16 p124). Figure 12 shows the tetrad distribution maps for Holly Blue for the 1995-2003 period (Frost, *loc. cit.*), for the period 2004-2017 and the comparison between the two periods. By 1995-2003 it was firmly established in VC63, up into 20km short of the northern borders of Yorkshire covering the Yorkshire Coalfield, Vale of York, the Humberhead Levels and most of VC61 except the Wolds (Figure 12: Top-left). Areas of partial colonisation included almost all of Yorkshire shy of the under-recorded farther reaches of VC65. By 2004-2017 (Figure 12: Top-right) there had been little change in distribution, with the exception of a strengthening in Middlesbrough in the Tees Lowlands (possibly arising from a *southwards* movement from colonies in Durham and Northumberland). Comparisons of the gains and losses in Holly Blue between the 1995-2003 and 2004-2017 periods show similar numbers and patterns across Yorkshire (Figure 12: Bottom-left and bottom-right respectively).

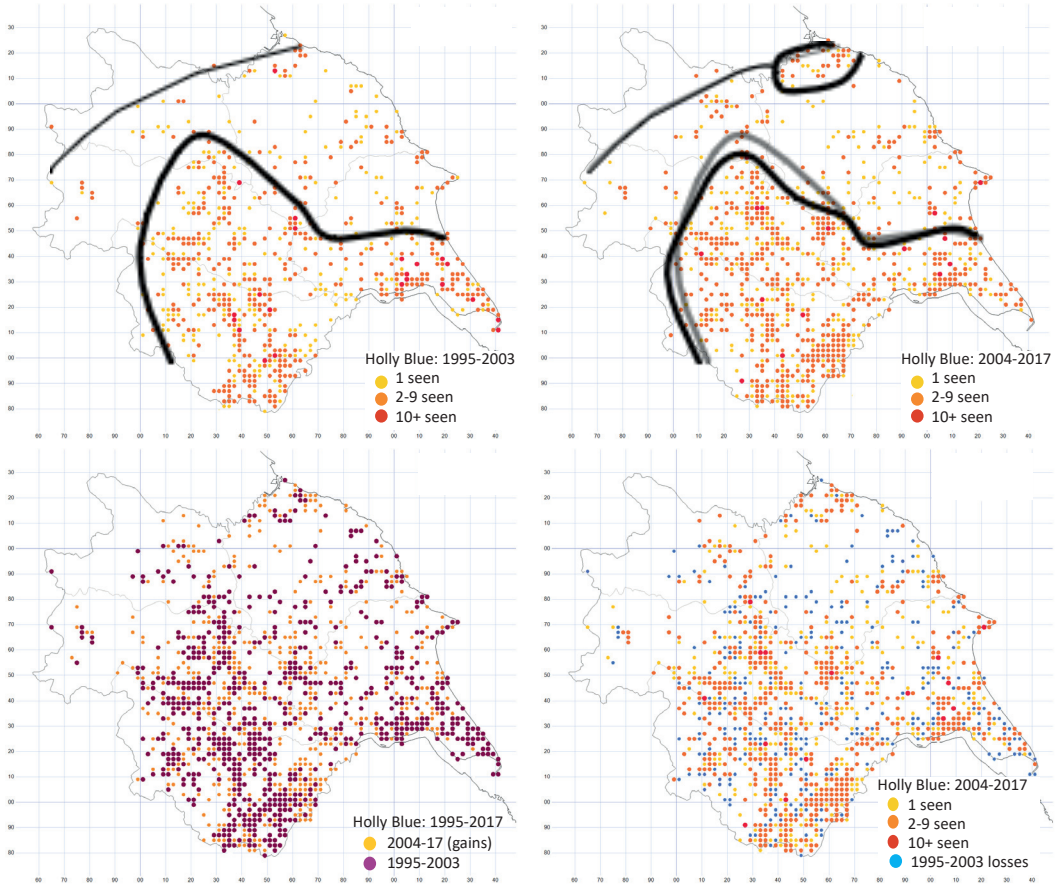

Figure 12. Tetrad distribution maps for Holly Blue *Celastrina argiolus*. Top-left: 1995-2003. The survey period reported in Frost (2005). Holly Blue present in 683 of 3232 recorded tetrads (=21.1%). Top-right: 2004-2017. Holly Blue present in 887 of 3720 recorded tetrads (=23.8%). Comparison between 1995-2003 and 2004-2017 with gains (Bottom-left) and losses (Bottom-right). Please see Figure 2 for further details.

Density maps for Holly Blue records for the survey periods 1995-2003 and 2004-2017 are shown in Figure 13. Again there is a good match in patterns between boundary lines drawn by eye (Figure 12) and the computer-generated density maps (Figure 13). The 1995-2003 density map shows strong presence of Holly Blue in the gardens of Hull and surrounding areas; by 2004-2017 Holly Blue has also strengthened in the midland town gardens. Increases in number of reports (as shown by number of white dots) acting as a proxy for abundance, show some increase between the two survey periods. The surface areas calculated were 11,150km^2 and 9,715km^2 for the *strong-90* and *weak-99* habitat regions respectively for Holly Blue in 1995-2003. For Holly Blue 2004-2017, the surface areas calculated were 10,650km^2 and 8,754km^2 for the *strong-90* and *weak-99* regions respectively. There has been some retraction in the distribution of Holly Blue as shown by drops both in *strong-90* and *weak-99* habitat surface areas.

Figure 14 plots the number of tetrads in Yorkshire where Holly Blue was seen as a function of

recording year. The solid line is the best-fit linear regression where there has been a correction applied to the number of tetrads recorded from within a given year. Tetrads recorded (corrected) is not significantly related to recording year ($r(23) = 0.006$, 95% CI [-0.503, 0.517], $p = 0.980$). There has been no change (< 1%) in tetrad coverage between the two survey periods of 1995-2003 and 2004-2017.

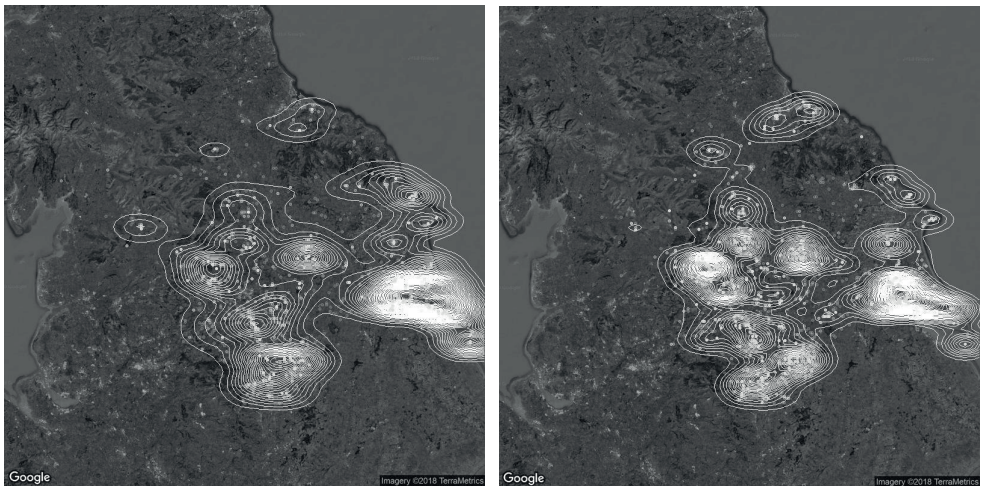

Figure 13. Holly Blue density maps overlaid over Yorkshire for the survey period 1995-2003 (left) and 2004-2017 (right). For explanation of maps please see Figure 3.

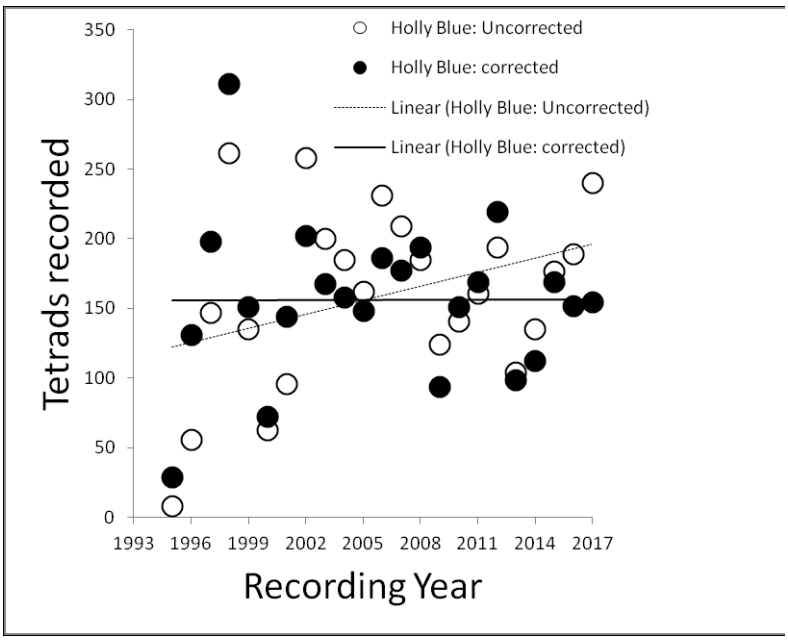

Figure 14. Number of tetrads in Yorkshire where Holly Blue was seen, as a function of recording year.

Essex Skipper (Fig.16 p124). Figure 15 shows the tetrad distribution maps for Essex Skipper for the 1995-2003 period (Frost, *loc. cit.*), for the period 2004-2017 and the comparison between the two periods. By 1995-2003 there were two minimal incursions from the south; a slim finger extending north-west for about 20km from Doncaster in VC63 where Essex Skipper was locally present and a colony at Spurn NNR (Figure 15: Top-left). By 2004-2017 (Figure 15: Top-right) the south-east border region of VC63 had been colonised (albeit at a low density) and the north banks of the Humber with high numbers recorded especially around Sunk Island in 2017 (by Sean Clough).

Most of the expansion of Essex Skipper appears to have occurred (or been noticed) since 2015 (Beaumont *et al*., 2016, 2017, 2018). Essex Skipper was spotted in July 2015 north of Middlesbrough (in VC66) and recorders were asked to take extra pains to check Small Skippers *Thymelicus sylvestris* (Smith, 2015). We must remember that Essex Skipper is quite hard to distinguish from Small Skipper (differing principally in the colour of the underside-tip of the antennae) and is thus easily over-looked. Increased vigilance when recording butterflies did not turn up Essex Skipper in VC62 but did lead to the detection of spread from known sites in the southern parts of Yorkshire. The area of potential colonisation is flung out north-west from the known areas of strong presence, with a width of about 40km in the far west of VC63 narrowing down to just a few kms before meeting above Goole. There are very few losses and many gains indicating a period of current expansion for Essex Skippers albeit in small numbers (Figure 15: Bottom row).

Density maps for Essex Skipper records for the survey periods 1995-2003 and 2004-2017 are shown in Figure 17. The data for 1995-2003 failed to provide contour lines in the density map because there were too few reports for the algorithm to reliably enclose an area. Therefore, the *strong-90* and *weak-99* habitat regions could not be calculated. For Essex Skipper 2004-2017 there were more records, therefore the density maps were created and the surface areas calculated were 6,288km^2 and 8,433km^2 for the *strong-90* and *weak-99* regions respectively.

Figure 18 plots the number of tetrads in Yorkshire where Essex Skipper was seen as a function of recording year. The solid line is the best-fit linear regression where there has been a correction applied to the number of tetrads recorded from within a given year. Tetrads recorded (corrected) is significantly related to recording year ($r(23) = 0.689$, 95% CI [0.522, 0.840], $p < 0.001$). There has been a seven-fold increase in tetrad coverage between 1995-2003 and 2004-2017. However, it can be seen that there are two distinct phases of growth: negligible growth between 1995-2014, followed by a steep increase in recorded tetrads between 2015-17 (marked respectively 1 and 2 in Figure 18).

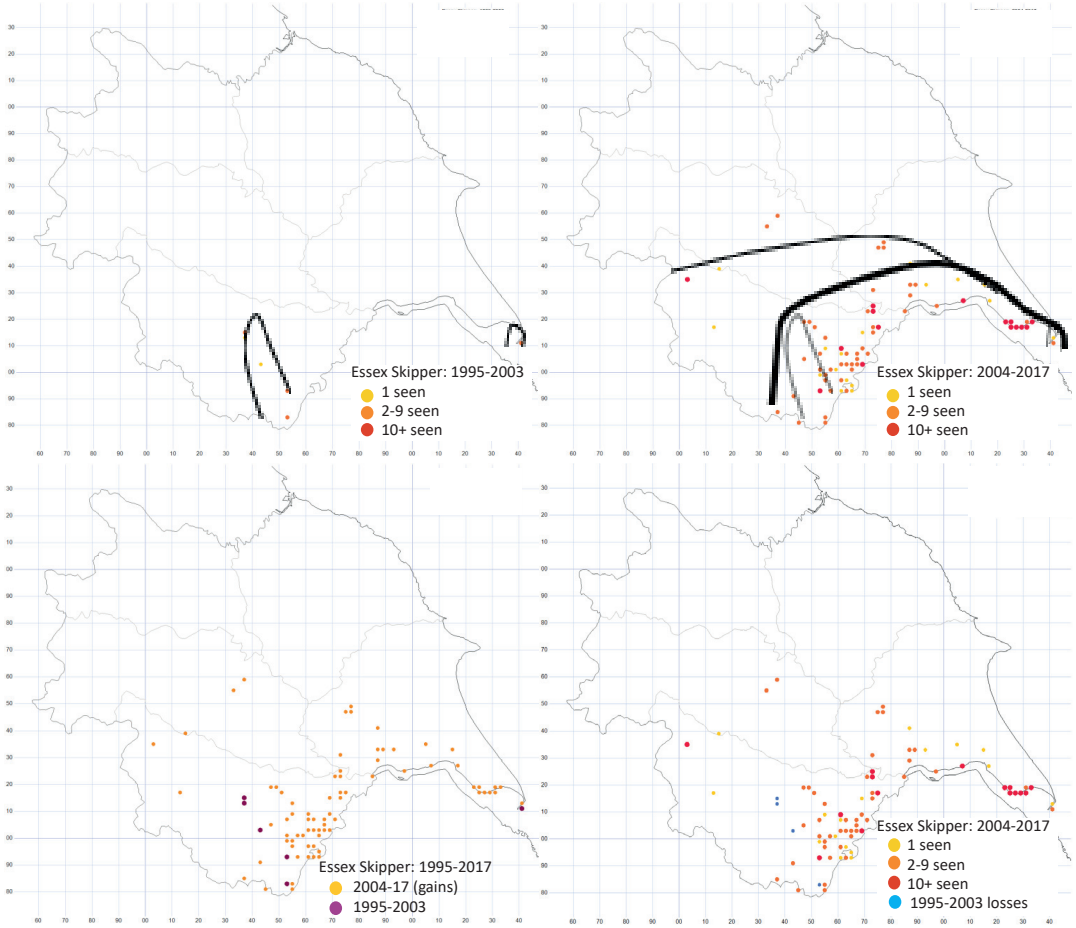

Figure 15. Tetrad distribution maps for Essex Skipper *Thymelicus lineola*. Top-left: 1995-2003. The survey period reported in Frost (2005). Essex Skipper present in 6 of 3232 recorded tetrads (=0.02%). Top-right: 2004-2017. Essex Skipper present in 76 of 3720 recorded tetrads (=2.0%). Comparison between 1995-2003 and 2004-2017 with gains (Bottom-left) and losses (Bottom-right). Please see Figure 2 for further details.

Figure 16. *Left*: Holly Blue *Celastrina argiolus.*
Right: Essex Skipper *Thymelicus lineola*. Note the black underside of the antenna tips which distinguishes it from Small Skipper *Thymelicus sylvestris*.

Figure 17. Essex Skipper density maps overlaid over Yorkshire for the survey period 1995-2003 (left) and 2004-2017 (right). For explanation of maps please see Figure 3.

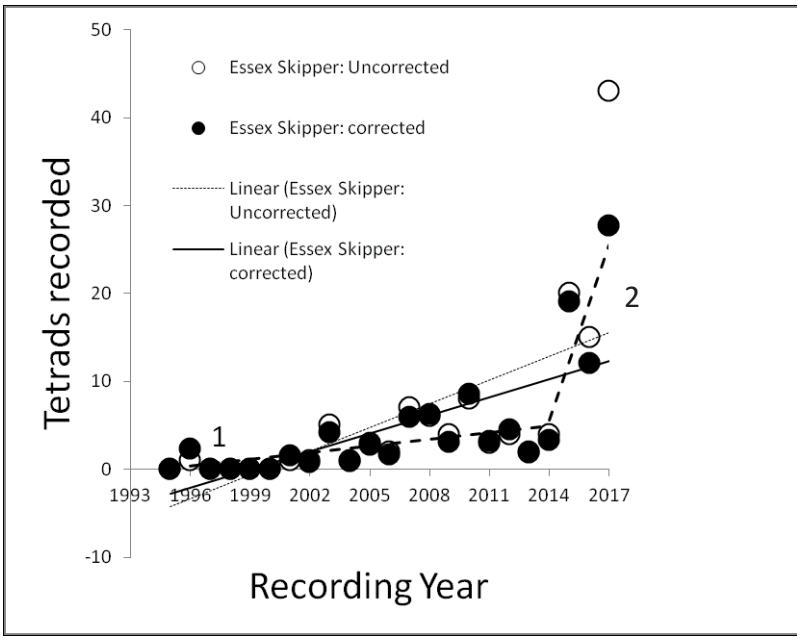

Figure 18. Number of tetrads in Yorkshire where Essex Skipper was seen, as a function of recording year. Two distinct phases can be discerned: negligible growth (1995-2014) and then rapid growth (2015-2017) marked respectively 1 and 2.

Discussion

The five recent lepidopteral colonisers identified in Frost (*loc. cit.*) have had a mixed recent history since Frost's 1995-2003 survey period. Speckled Wood has spread throughout most of Yorkshire and is only relatively limited now in the Vale of Pickering (VC61/62), the northern Wolds of VC61 and western VC64 (Figures 2-4). Gatekeeper has remained largely contained in

its original strongholds, with some indication of partial colonisation (Figures 5,7,8). Comma has filled in and merged its two strongholds in the south and south-east of Yorkshire. It has also strengthened in VC62 and in the south-east of VC65 (Figures 9-11). Holly Blue shows no change in distribution since 1995-2003; the only wrinkle is a strengthening around Middlesbrough (Figures 12-14). Finally, Essex Skipper has only shown any expansion since about 2015 when it has spread further into VC63 and VC61 from toeholds established in 1995-2003 (Figures 15,17,18).

When butterflies contract or expand in range they do so dynamically in time; a good summer might see a sudden range expansion which is stalled by a poor summer. There are periods of consolidation when numbers build over a number of years within pre-existing regions of strong presence. Then there might be a burst of sudden expansion. Some butterflies are subject to periodic predator-prey cycles that cause large fluctuations in butterfly numbers; for instance, Holly Blue numbers cycle up and down every 4-6 years as the parasitic wasp *Listrodomus nycthemerus* periodically overwhelms the caterpillar population though this particular ichneumon has never been recorded in Yorkshire (W.A. Ely, pers. comm.). Looking at longer periods of time than a year blurs and essentially loses this information. However, it could be argued that using range distribution maps based on longer time periods (1995-2003 and 2004-2017) reveals medium range shifts that are more meaningful. For instance, a poor summer and a good summer cancel out; a run of good summers (or poor summers) might underpin sustained range expansion (or retrenchment). Time periods of around a decade are probably more digestible and understandable for us as humans to appreciate – that an area had no Speckled Wood once, and now it has a firmly established population, can take a decade to happen and that is something that registers with us.

The (spatial) analysis level of this report is also firmly regional. If the report had a finer level of granularity then the analysis might have captured those aspects of expansion and retraction in range that are driven by availability of host plants and suitable habitat (for instance, see Suggitt *et al*., 2011). This report adopts again a half-way house – a large enough scale to encompass general movement (such as the suggestion of north-west movement in most of the butterfly species in this report) but small enough to capture and notice intra-regional spread at the level of NCAs. It is also the case that the five butterfly species reviewed in this report are wider countryside butterflies so they will be less affected by issues of habitat suitability than if they were habitat specialists (such as Northern Brown Argus *Aricia artaxerxes*).

When the *Butterflies of Yorkshire* was published (Frost, *loc. cit.*), one might have been tempted to imagine that the northwards expansion of recent colonising butterflies would proceed unabated in the next two decades. This has not been the case – the story is a complicated nuanced one at the local level for Yorkshire – only Speckled Wood and, most recently, Essex Skipper – have spread prodigiously (and for Essex Skipper only in the last three years). When Frost was publishing there had been sustained increases in central England temperatures of 1.5^{o}C between 1976 and 1998 (Roy & Sparks, 2000) which presumably drove the northwards expansion of the lepidopteral colonisers at the very end of the millennium. However, between 1995 and 2014 there has been no discernible shift in mean spring, summer, autumn or winter temperatures in Yorkshire (Smith & Smith, 2014). The years 2015-2017 have included the warmest two years globally on record – nevertheless, even factoring these additional years

into the temperature series between 1995 and 2017 reveals no significant shift in mean spring, summer, autumn or winter temperatures in Yorkshire [spring, $r(23) = -0.092$, 95% CI [-0.529, 0.343], $p = 0.678$ *NS*; summer, $r(23) = 0.005$, 95% CI [-0.411, 0.420], $p = 0.984$ *NS*; autumn, $r(23) = -0.171$, 95% CI [-0.535, 0.330], $p = 0.436$ *NS*; winter, $r(23) = 0.319$, 95% CI [-0.05, 0.719], $p = 0.138$ *NS*]. This is interesting as it suggests that further expansion was possibly attendant on sustained temperature increases at least for Gatekeeper, Comma and Holly Blue. The summers have been increasingly dull and overcast and this may also limit expansion – in this respect, it is not surprising that Speckled Wood, which is tolerant of shade, has been the greatest beneficiary of the last two decades.

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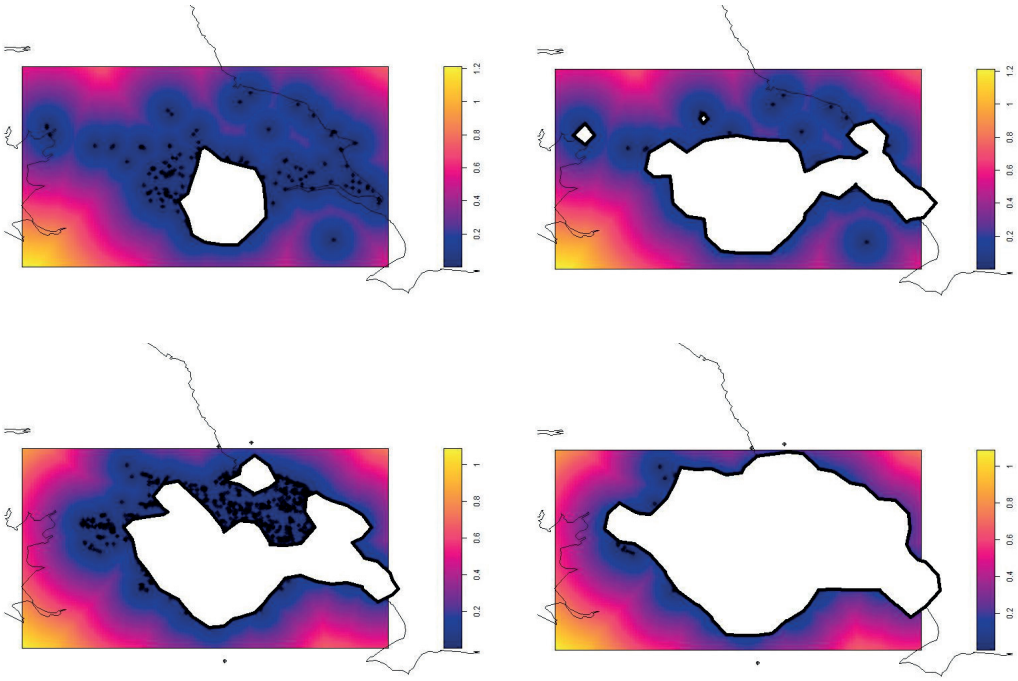
Appendices

Figure Appendix 1. Speckled Wood continuous heat maps overlaid over Yorkshire for the survey periods 1995-2003 (first row) and 2004-2017 (second row). Individual records of Speckled Wood are shown as black crosses, with multiple records being overlaid on top of each other (which will influence the heat map colouring). The heat maps are analogous to the density maps (see Figure 3) and represent the possibility of seeing a Speckled Wood in a location based both on the recorded presence and number of reports of that butterfly in that location plus the surrounding regions. Colour coding shows high density (blues) to low density (yellow). The bold black solid contour lines surrounding the filled-white regions bound an area defined as the *minimum* area in which there is a specified probability of encountering a butterfly.



The bounding contour line in the first column encloses an area within which there is a 90% probability of the butterfly being encountered – this is the 'strong' presence area denoted *strong-90*. The bounding contour line in the second column encloses an area within which there is a 99% probability of the butterfly being encountered – this is the 'weak' presence area denoted *weak-99*. Thus the top-left figure is *strong-90* presence in 1995-2003, top-right is *weak-99* presence in 1995-2003, bottom-left is *strong-90* presence in 2004-2017, and bottom-right is *weak-99* presence in 2004-2017.

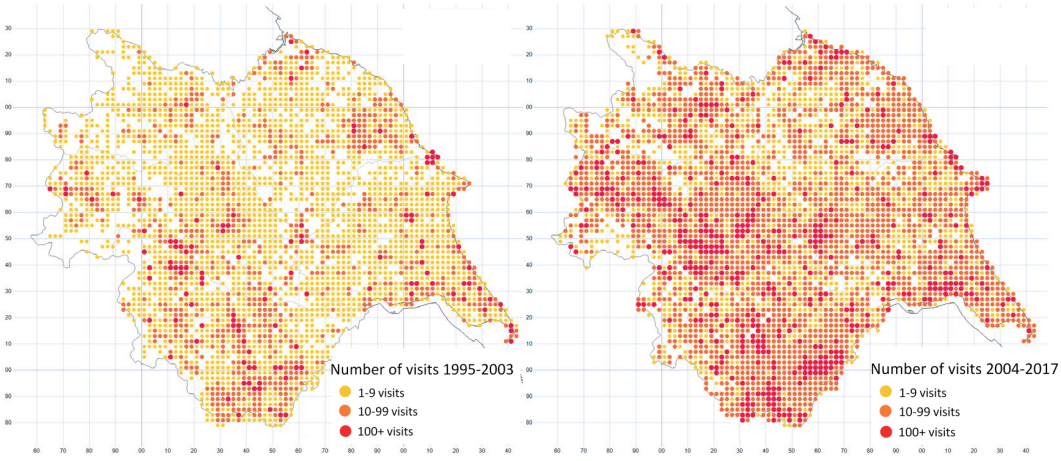


Figure Appendix 2. Levana maps showing recorder effort by number of visits to each tetrad. Left: 1995-2003. Based on 158,931 records and 3224 tetrads visited (=78% of Yorkshire visited). Right: 2004-2017. Based on 488,428 records and 3695 tetrads visited (=90% of Yorkshire visited).