How well has BSBI chronicled the spread of neophytes?

M. E. BRAITHWAITE

Clarilaw, Hawick, Roxburghshire, TD9 8PT

BACKGROUND

This paper is adapted from a Presidential Address delivered at a BSBI conference on *Understanding our Alien Flora* in London on 25 October 2008 that was illustrated using PowerPoint. It offers an overview and discussion partly supported by fieldwork. The graphical treatment of historical trends is deliberately simplistic, though reference is made to research papers with statistical content.

ABSTRACT

Following an overview of the main processes of dispersal, the limited chronicle available by considering two 'snapshots in time' in the spread of neophytes in Britain is considered in relation to the *New Atlas* and the *BSBI Local Change* project as reported in *Change in the British Flora 1987–2004*. In search of a 'slow-motion movie' of spread on a year-by-year basis, some dramatic recent changes observed by the author in Berwickshire are examined, especially colonisation by *Spergularia marina*. The chronicle of spread proves to be an inadequate to distinguish between the two main mathematical models, radial spread and exponential spread. A classical study of *Galinsoga* is re-examined. Generalisations are drawn on what can be expected from BSBI's recording strategy. A detailed study of the colonisation of the Scottish Borders by a bird, *Sitta europaea* (Nuthatch), is used with the other studies as a basis for comment on the patterns of spread observed. *BSBI Local Change* is revisited in search of estimates of the time neophytes have taken to reach a mature distribution. The very modest extent to which the models can be used to predict the future is noted.

KEYWORDS: British Flora, Alien, Colonisation, Distribution, Mathematical Model.

INTRODUCTION

Our conference today is on alien plants, or incomers as I prefer to call them to avoid being judgemental. It's the more recent arrivals or neophytes (species first recorded in Britain after 1500) that are the main focus of attention. As one starts talking about them it is their spread that one soon comes to: how far and how fast? I find that this is a big subject to get one's head round, and one that BSBI is not as good at as I'd thought. It's not just maths: there's botany too.

Questions one might like answers to include

- What are the main processes of dispersal?
- What distribution pattern can be expected as spread advances?
- Does the rate of spread change?
- How fast do species spread?
- Can distributions be estimated into the future?

I deal with these in turn.

THE PROCESSES OF DISPERSAL

The direct seed rain from a plant to the ground gives very limited dispersal and more effective dispersal depends on hitching lifts: from the wind, on water, on ants, animals (including us humans) or birds, on vehicles, packed in goods as seed impurities or as weeds in plant containers. In general one can only guess at which processes are most important for particular species as direct observation is difficult.

Some of these examples are rare events, but they nevertheless seem to be crucial in driving long-range dispersal. One may reflect further on the balance between short-distance and long-distance dispersal. Human dispersal is of various kinds. If a seed sticks to the outside of a vehicle, short-distance dispersal is likely to predominate. If a seed or seedling is carried in goods as a seed impurity or container-plant weed the dispersal area will depend on the product but may be Britain-wide.

From the point of view of the plant the optimum outcome for success is to be the crop itself, being a stowaway is a good second best. The suspected spread of *Anisantha diandra* in *Triticale* seed used as a game crop may be a current example of a successful stowaway (all Latin names follow Stace 1991).

THE DISTRIBUTION PATTERN AS SPREAD ADVANCES

BSBI specialises in snapshots in time of the distribution of a species, perhaps 40 years apart like the maps in the two *Atlas* surveys (Perring & Walters 1962; Preston *et al.* 2002). The snapshots are 'fuzzy' in time as the recording is done over a span of years.

Conyza canadensis is typical of species increasing between the dates of the two *Atlases*. Alas, this is not apparent in the *New Atlas* map which shows presence as an alien in 974 hectads in the 1987–1999 dateclass and only 95 hectads in earlier dateclasses as it is the most recent record that is mapped, so one must turn to the first *Atlas* as well to learn something of its spread. One finds it had been recorded in 571 hectads by 1962, so its range (the number of recording units in which it was found) has almost doubled in 40 years.

It is only because the inland records of *Spergularia marina* are treated as alien that one can infer the recent spread of this species from the coast along verges from the *New Atlas* map. It is shown as present in the 1987–1999 dateclass in 688 hectads as native and 366 as alien.

Studying the spread of plants is like studying how a horse gallops: one needs a slow-motion movie, not just snapshots, to understand the process. So the *Atlas* maps alone are insufficient for this purpose. *BSBI Local Change* (Braithwaite *et al.* 2006) was an improvement as each survey was a sharp snapshot in time, completed in just two years. But as yet, like the *Atlas*, it has only been repeated once so one doesn't have a data series over time. Nevertheless the eye is good at getting the feeling of a movie from just two snapshots and the *Local Change* maps do have a sense of movement.

Conyza canadensis doubled its range at tetrad scale in the 16 years between the two *Local Change* surveys (Fig. 1). The grey dots, observed in both surveys, are mainly clustered together but there are outliers also. The black dots, found in the second survey only, show infilling of the core range and spread. The spread is mainly outwards from the outliers (even allowing for some bias as the second survey was more intensive than the first). There are some new black outliers, but not many. So one has the impression of a species spreading by rare long-distance events of, say, 100 km

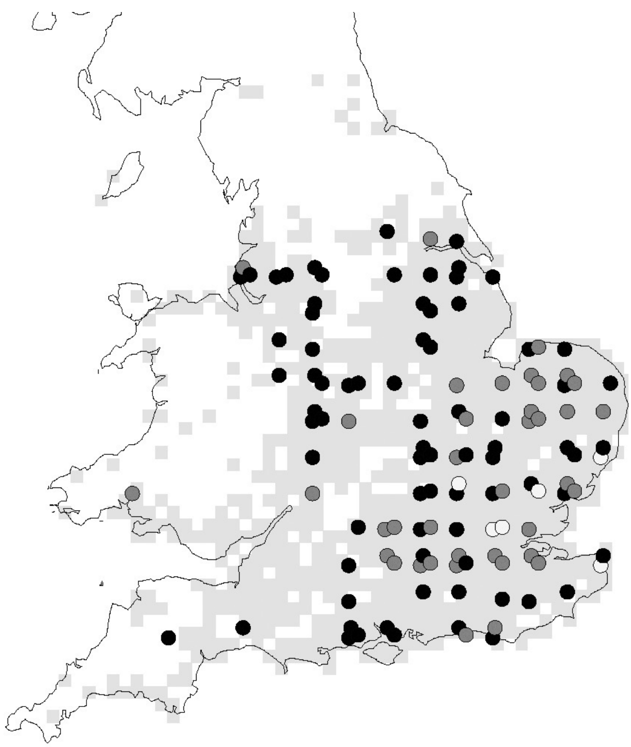

FIGURE 1. *Conyza canadensis.* ● 2003–2004 only, ○ 1987–1988 only, ● Both Surveys
Light grey background *New Atlas* survey 1987–1999.

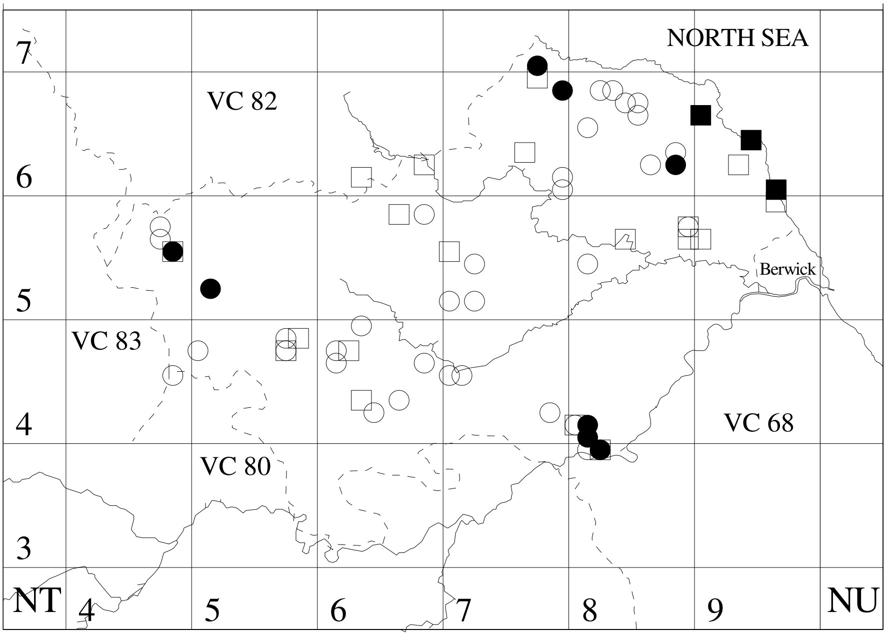

FIGURE 2. The distribution of *Spergularia marina* (*Lesser Sea-spurrey*) in v.c. 81. First recorded ● 1992–1993 ■ 1994–1995 ○ 1996–1997 □ 1998–1999.

and much more frequent short-distance events, say up to 10 km.

But there is a degree of illusion because *Local Change* surveyed only a 1% sample of the countryside so the balance of long-distance events may be rather different to appearances.

I have searched the BSBI MapMate database for v.c. 81 Berwickshire and the wider BSBI literature for data that gives more of the feeling of a movie. Such data is hard to find. Here are some contrasting examples.

Spergularia marina has colonised Berwickshire in less than 10 years (Fig. 2). There is not much doubt that this annual species is spread by seeds hitching a lift on the outside of vehicles and as a contaminant of the road-salt itself. It is found at the road verge where large colonies can easily be seen from a car at 60 mph. If I had really wanted to, I could have surveyed all the main roads of Berwickshire each year as it spread. I wasn't as systematic as that as the record shows.

This species arrived in Berwickshire from the south, as that is where earlier records were made. All the 1992–1993 Berwickshire records are on main roads from the south. The extra records in 1994–1995 are on the A1, not by the shore. In 1996–1997 a special survey covered pretty much all the main roads, not every kilometre was searched but the plant was by no means everywhere. By 1998–1999 the species became more or less ubiquitous on the main roads and began to spread to minor roads. The coverage in this period is far from complete.

This pattern of recording is, I believe, fairly typical of what BSBI recorders do. There is a flurry of interest after the first record in an area, often picking up spread that had occurred some time earlier, followed by a loss of interest. Thereafter the flow of records depends on the pattern of general recording activity in the v.c.

The mapped pattern of spread is striking: there has been a mixture of long-distance events and short-distance bulking up. One wonders what mathematical model best describes this pattern.

THE MATHEMATICS OF SPREAD

There are two basic mathematical models of spread:

- Radial spread, like the ripples on a pond after a stone is thrown in, models a species spreading outwards as a wave-front from a point of introduction
- Exponential spread models a species spreading at random within an area with new colonies not clustering together

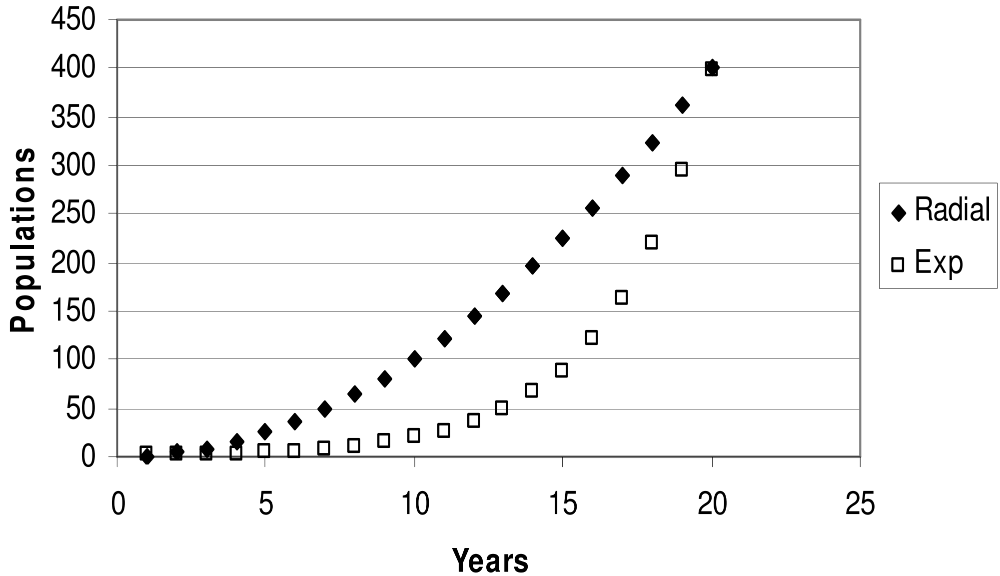

FIGURE 3. Radial and Exponential models compared.

There is some expectation that natural dispersal from a seed rain (even if assisted by wind or animals) will progress in a more or less radial manner. In contrast some sorts of human dispersal (whether intentional or unintentional) might be expected to be near-exponential, with distance no barrier (within Britain). A mixture of dispersal mechanisms might be expected to lead to a pattern of spread intermediate between these two extremes.

The chart (Fig. 3) compares growth from one population to 400 populations after 20 years for the two models. Radial growth reaches 100 populations after ten years while exponential growth is still down at about 20 populations. So there is quite a contrast in the pattern of growth predicted by the two models and one might expect to be able to distinguish them in survey data or to point to an intermediate.

Spread does not of course continue indefinitely. Sooner or later suitable uncolonised habitat begins to run out and spread slows. The mathematics to cover this is quite simple but need not detain us here as the outcome is much as one would guess. In practice it can be difficult to tell if spread is slowing because habitat is running out or because the pattern of recording has changed.

Returning to the spread of *Spergularia marina* in v.c. 81, the data is plotted in figure 4. One tests the fit of data to an exponential model by taking the log of the cumulative records and seeing if one gets a straight line, for a radial model one takes the square root. Note that in this chart the scale of the y-axis is different for the two sets of data. The division of the regression lines plotted into two is a speculation based on recorder behaviour: it is not supported statistically.

Disappointingly the data just isn't good enough to distinguish between the two models. The discontinuity after 1999 mainly reflects a change in recorder behaviour both because of loss of interest with the species and because the *New Atlas* survey was over. But there was a change in habitat too: the main roads were more or less fully colonised and the species adapted to colonise minor roads.

The apparent adaptation to colonise minor roads is highly intriguing. There is a possibility that it signals a real genetic change to enable the species to thrive in more eutrophic conditions. If true, this would imply a second wave of colonisation superimposed on the first. I have not observed this in *Spergularia* but have seen something of the sort in *Cochlearia danica*.

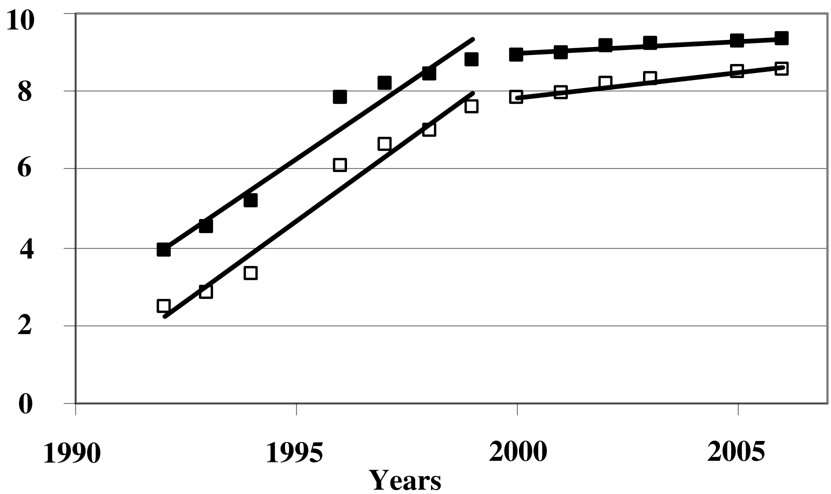

FIGURE 4. The spread of *Spergularia marina* in v.c. 81 (inland records only). ■ Fitting to an exponential model (y axis = 5 × $\log_{10}$ cumulative 1 km squares). □ Fitting to a radial model (y axis = square root cumulative 1 km squares).

Matricaria recutita is a species that has enjoyed a vogue of popularity with the highway authorities and has been sown in quantity along new roads and motorways (I have observed this by the A1 in Yorkshire and near Melrose and Hawick in the Scottish Borders). Not surprisingly it has turned up in arable land in areas where it was unknown, including v.c. 81. There it has sometimes prospered and its success may also owe something to warmer summers. Whether the increase between the two *Local Change* surveys will be maintained is thus an open question.

The exponential graph appears to give a promising fit to the Berwickshire data (Fig. 5). But, as this is my own data, I know that my recording pattern changed in 1987 when a new cycle of recording commenced that ran to 1999. The radial plot seems to match that, so again the data is inadequate to separate the two models.

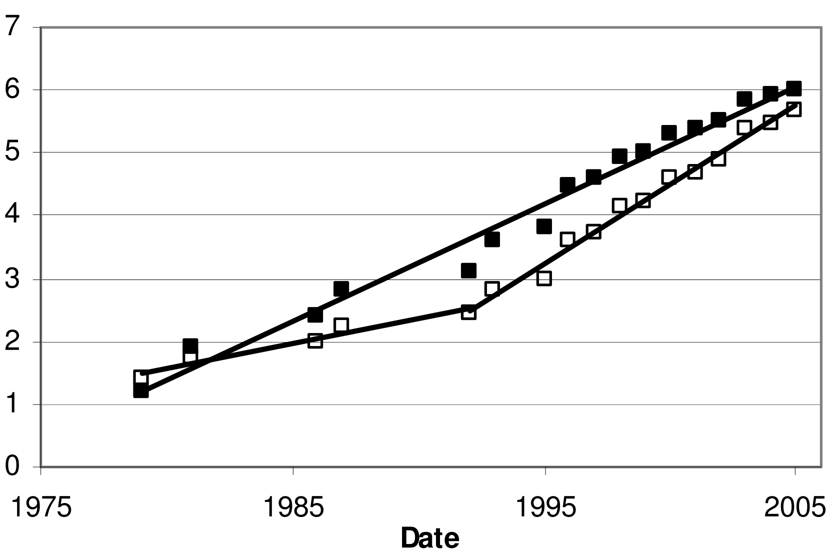

FIGURE 5. The spread of *Matricaria recutita* in v.c. 81. ■ Fitting to an exponential model (y axis = 4 × $\log_{10}$ cumulative 1 km squares). □ Fitting to a radial model (y axis = square root cumulative 1 km squares).

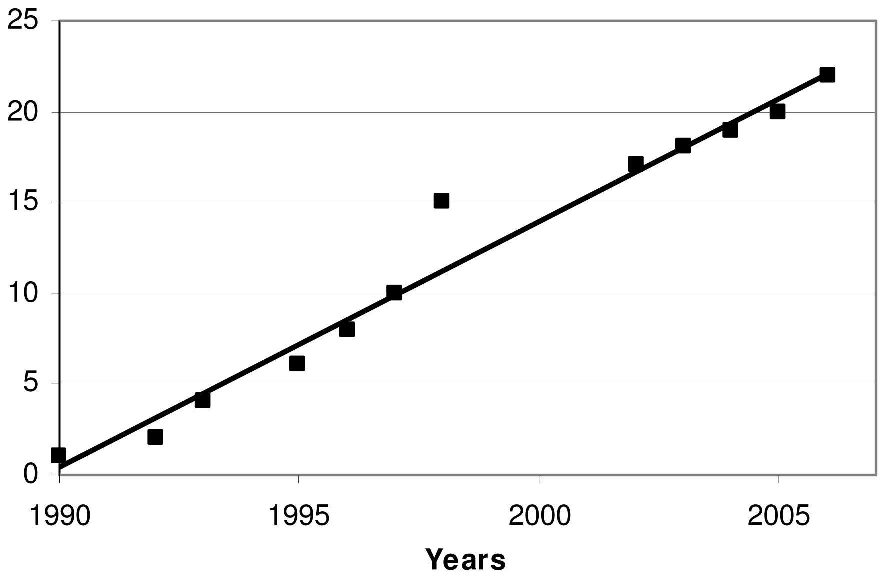

FIGURE 6. *Verbascum thapsus* in v.c. 81. ■ Fitting to an arithmetic model (y axis = cumulative 1 km squares).

Verbascum thapsus is quite scarce in v.c. 81 and suspected of being an incomer that is casual in at least some of its localities so I was interested to see if I had any evidence one way or the other.

The apparent fit to an arithmetic model (Fig. 6) points to a steady build up of records with no evidence of spread or decline. This could indicate either that the localities of this scarce plant were only gradually being discovered over time or that the plant is a casual, new localities being picked up at random (with no field check as to whether old localities are still present). To investigate this I made a resurvey of a 50% sample of the sites in 2008. There was an almost equal divide between sites where the plant was still present and seemed more or less permanent and those where it was not still present and where the original occurrence seemed to have been casual.

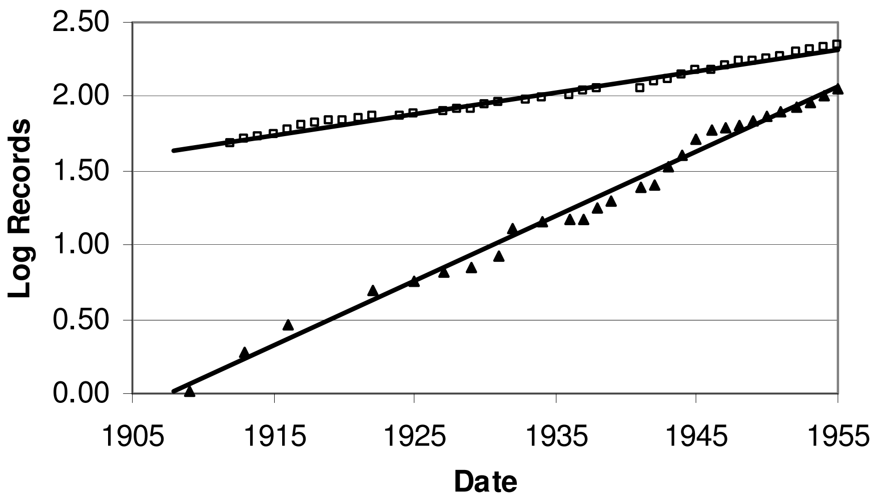

FIGURE 7. The spread of two alien *Galinsoga* species in Britain, 1909–1955 (after Lacey). Fitting to an exponential model □ *G. parviflora* ▲ *G. quadriradiata.*

LACEY'S STUDY OF *GALINSOGA*

Two *Galinsoga* species, *G. parviflora* and *G. quadriradiata*, naturalised in Britain have built up a considerable literature. W. S. Lacey (Lacey 1957) presented data on the spread of *Galinsoga* to a BSBI conference in 1957 (Fig. 7). It appears to show a good fit between the cumulative 'new locality' records for each of the two species and an exponential model.

Prof Mark Williamson, who has been studying the mathematics of spread for some years (Williamson *et al.* 1996, 2003, 2005), does not like this dataset at all. For one thing it goes against strong evidence for the radial spread for these species that he has found by studying a fine set of data from the Czech Republic where recording coverage has followed a steady plan continued over many years. For another thing he distrusts Lacey's 'Localities'. He thinks they are too imprecise to have much meaning. He seeks consistent repeat survey using hectads, tetrads or monads. BSBI does not have that sort of data, so I have been interested in seeing whether more can be read into Lacey's data despite its shortcomings.

I have now fitted the data to a radial model (Fig. 8). The result is interesting as it seems that a radial model is roughly supported if a discontinuity is accepted from 1939. This is highly probable as that is just when Lacey and his correspondents took up the study. They had noticed that *G. parviflora* had spread remarkably on bomb sites during the war. Interestingly Salisbury suggested that the pappus on *Galinsoga* is rather inefficient and that it needed an explosion to lift the seeds high enough in the air to be wafted effectively by the wind. As is so often the case, real change on the ground led to increased recorder effort and the one confuses the other.

With regard to scale, I infer that Lacey's 'Localities' were not too far removed from tetrads, as that is my experience with historical records localised by place names. The trouble is that there is no suggestion that all tetrads in a given area were systematically surveyed year by year, quite the contrary.

But what Lacey and his correspondents did is just what BSBI recorders still do, so there is no point in blaming Lacey.

I have tried looking at the spread of *Galinsoga* at v.c. scale from first v.c. records. There is apparent support for a radial model, but the number of datapoints is low, and there is always the possibility that the failure of the log graph to hold straight may reflect the fact that uncolonised v.cc. with suitable habitat may be running out.

Further studies of spread reported in BSBI journals include those of *Veronica filiformis* (Bangeter & Kent 1957) and *Epilobium ciliatum* (Preston 1988). They have similar limitations.

So what do we in BSBI need to do if we wish to chronicle the pattern of spread of neophytes more accurately? Maybe we need to examine our v.c. tetrad flora data to see if we have examples where a more or less constant

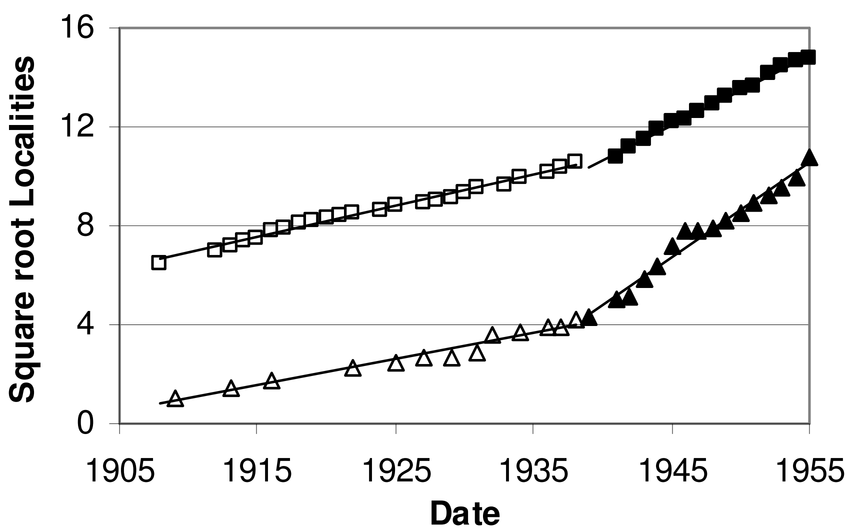

FIGURE 8. Fitting to a radial model. □ ■ *G. parviflora* Δ▲ *G. quadriradiata.*

number of tetrads were surveyed each year over a period and seek interesting trends for some of the increasing species. Success might encourage others to record more systematically in future. But we need to be very wary of the effects of changes in recorder effort as highlighted above and in a series of papers by T. C. G. Rich, starting with his report on the *BSBI Monitoring Scheme* 1987–1988 (Rich & Woodruff 1990). His 1996 paper in *Watsonia* begins with a useful overview (Rich & Smith 1996).

NUTHATCH IN THE SCOTTISH BORDERS

My search for better data has led me away from plants to a bird. *Sitta europaea* L. (Nuthatch) has colonised the Scottish Borders in less than 20 years. This is a very sedentary bird that prefers to spend its whole life in a single territory; even its brood won't disperse more than they have to. R. D. Murray and The Scottish Ornithologists' Club (Murray 2008) have chronicled its spread in amazing detail, though as it is found mainly in parks and gardens it is relatively easy to spot. Their data is so good that aggregate data for each three-year period between 1989 and 2006 gives six maps at tetrad scale with broadly complete coverage. These maps really do amount to a movie.

Nuthatch spread into the Scottish Borders from the south along the east coast as the Cheviot Hills block off almost all other points of entry for such a lowland bird. Nevertheless the new colonisation was soon surprisingly well-scattered across the region. As colonisation progressed there was a mix of scatter to new areas and filling-in around early records representing dense colonisation of favoured habitats. By 2006 nearly all suitable habitat had been colonised (189 tetrads in 43 hectads), so subsequent spread is bound to be more modest.

The parallel between the pattern of spread in nuthatch and in alien plants is striking. There is the same sort of mix between long-distance and short-distance dispersal. Plant seeds 'fly' a long way when they can hitch an especially good lift and fan out when they get more modest help in dispersal.

The Nuthatch data, unlike the plant data, did seem to be good enough to expect a fit to one of the two models. At hectad scale the radial model (R^2 = 0·963) fits much better than the exponential model (R^2 = 0·890) while at tetrad scale the two models give a similar fit (R^2 = 0·971, R^2 = 0·968). This is difficult to interpret. One reason for the imperfect fit to the mathematical models may be the fact that the spread of Nuthatch is limited to river valleys which are not randomly distributed across the landscape. There is a suggestion in the tetrad data that the spread is initially exponential (random long-distance dispersal predominating) and then radial (short-distance dispersal predominating), but this has not been supported statistically.

The radial dispersal observed in plants and the nuthatch does not look very much like the ripple on a pond as there are outliers ahead of the main wave front, but mathematically it is still an expanding wave front, albeit one with what is known as a 'thick tail'. Williamson (Williamson *et al.* 2005) has demonstrated that some species do spread exponentially for a while if they get particularly good at hitching lifts, but they are the minority. But it may be unproductive to dwell too much on the mathematical issues: more interesting perhaps is the suggestion of a complex mix of long-distance and short-distance dispersal events. The com-plexity is reassuring: it would not be easy to believe that plant dispersal followed one or two simple patterns when so many processes are at play.

I suggest that the species most likely to spread exponentially for a limited period (and thus potentially very rapidly) are those that are cultivated, like *Veronica filiformis* in the past, or those that stowaway with cultivated plants either as weed seedlings in container-plants, like *Galinsoga* or *Cardamine corymbosa*, or as a seed impurity, like *Anisantha diandra* in *Triticale*.

BSBI LOCAL CHANGE

I have had a look at what *BSBI Local Change* can contribute to the subject of the spread of neophytes. It is not very much as there are only two surveys. However a third data point can be added as the date of first introduction.

At individual species level no statistically valid trends can be expected. However by looking for common patterns for a group of species points of interest emerge.

I have taken just the group of the best naturalised neophyte species, not affected by continuing introduction, separated as 'Group 1' in the *Local Change* report (Fig. 9). What one finds is that the spread of most of these species is slowing down or has stopped. Their

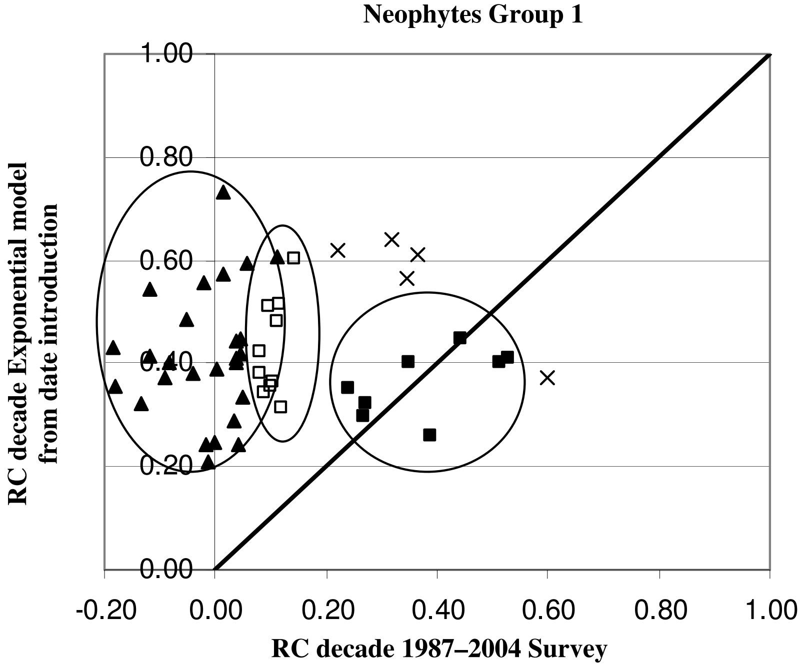

FIGURE 9. Fitting to an exponential model – Group 1. ▲ Mature □ Radial ■ Exponential × Other.

distribution is mature. This emphasises a limitation of the *Local Change* sample as it is only able to work with relatively widespread species. There is just not enough data in a survey of 1% of the countryside to learn anything about the spread of the very many scarce neophytes, and it is of course the scarce ones that one most wishes to study to see how fast they are spreading.

For those species in this group that are still spreading rapidly there is a suggestion in the data that some spread is exponential and that some spread is radial. However I cannot pick out any key characters that separate the two groups of species. So I will pass over this aspect and consider only the species with a mature distribution.

HOW FAST DO SPECIES SPREAD?

The 25 species in *BSBI Local Change* Group 1 Neophytes with a mature distribution have taken an average of 170 years to colonise Britain, or, to put it another way, a successful species might take between 100 and 200 years to spread across our country.

Their range at the end of that period will vary widely depending on the habitat colonised, climate and other factors. The range of the 25 species in this sample is currently between 4% and 80% of British tetrads.

The average rate of radial spread is about 0·7 km/yr, but this is based on the assumption that all the tetrads occupied lie in a solid circle on the map. Real distributions are always more scattered than this so a better estimate might be double this or 1·4 km/yr.

For exponential spread the average time to double the range is about 16 years.

These figures are of the same order of magnitude as Williamson's estimates from his Czech hectad-scale data of 1 km/yr and 10 years to double (Williamson *et al.* 2005). Some discrepancy between tetrad data and hectad data would be expected.

PREDICTIONS OF FUTURE DISTRBUTIONS

I finish with some wild speculation on what the future might have in store for three fast-spreading neophytes.

If *Claytonia sibirica* spreads at a radial rate of 1 km/yr it might reach 80% of the distribution of *Geum urbanum* by 2050, even though it is more restricted to woodland than that species.

If *Allium paradoxum* doubles its range every 16 years it might reach 80% of the distribution of *A. ursinum* by 2100, though it remains to be seen whether *A. paradoxum* will prosper in the west as it has in the east.

If *Lemna minuta* doubles its range every six years it might reach 80% of the range of *L. minor* by 2009, and every pond within a tetrad only a year or two later (though this provocative estimate relies on the validity of an estimate that *L. minuta* was so little known that it was recorded in 2003/2004 in only one third of the *BSBI Local Change* tetrads in which it was actually present).

CONCLUSIONS

Taken together, the Berwickshire studies of *Spergularia marina*, *Matricaria recutita* and *Verbascum thapsus* with Lacey's study of *Galinsoga* offer a sobering insight into the limitations of the usefulness of BSBI datasets in the study of spread in plants. BSBI has learned much about the current distribution of neophytes but less about the mode and pattern of spread. The Society relies on a body of volunteer recorders who perforce operate in ways that suit their circumstances. This leads to relatively short-term local flora projects at differing spatial scales that are not synchronised across Britain and Ireland. That is the reality and it leaves limited scope for the introduction of standardised recording practices. Neither of the two landmark *Atlas* projects relied exclusively on re-survey in a narrow date-class and at best can only provide two data points on a dispersal curve. Any attempt to look behind the summary data published to the underlying year-by-year records would be likely to come up against insurmountable inconsistencies.

Similarly the sample recording in Berwickshire has not been stratified sufficiently on a year-by-year basis across the vice-county to yield consistent results. Instead a hectad by hectad approach was adopted, and that only for the period 1987–1999 after which different survey priorities prevailed. If the study was extended to data from other vice-counties, further inconsistencies would be found. However, it might be possible to sample data from those vice-counties that have undertaken long-term tetrad mapping projects so that a stratified sample of tetrads recorded in each of a series of years was examined. Whether the series of years available would as yet be long enough to yield valuable results remains to be demonstrated, but I hope this paper may stimulate such studies.

The *BSBI Local Change* project, like the two *Atlases*, only provides two data points, so it will be many years before further repeat surveys can be hoped to provide an adequate chronicle of the patterns of spread.

As suggested above, dates of first vice-county records are perhaps worthy of further study, but the spatial scale of a vice-county is too great for the finer detail of the patterns of spread to emerge. Then it is only a minority of neophyte species that have been recorded consistently over a long span of years. Many even of the widely naturalised neophytes were absent from Bentham and Hooker and were first treated in Clapham, Tutin and Warburg's *Flora of the British Isles* (1952). Many of the species of horticultural importance were widely ignored until Stace's flora (Stace 1991) was published and the coverage of such species remained notably patchy in the *New Atlas.*

While BSBI datasets do have limitations these should be set in perspective against the remarkable success of the two *Atlases*. Their maps of *Veronica filiformis*, for example, do provide striking visual evidence of spread in a way that no graph can hope to. Moreover, when looking at a map, one can with experience compensate by eye for many of the recording deficiencies.

ACKNOWLEDGMENTS

Thanks are due to Professor Mark Williamson, Professor emeritus of Biology at the University of York for detailed comment on drafts of this paper and the supply of reference material and to Dr Chris Preston at C.E.H. Monks Wood, George Hutchinson at National Museum Wales and Dr Mark Spencer at the Natural History Museum, London for further help with reference material.

REFERENCES

BANGETER, E. B. & KENT, D. H. (1957). *Veronica filiformis* Sm. in the British Isles. *Proceedings of the Botanical Society of the British Isles,* **2**: 197–217. (1962). Further notes on *Veronica filiformis*. *Ibid*. **4**: 384–397. (1965). Additional notes on *Veronica filiformis*. *Ibid.* **6**: 113–118.

BRAITHWAITE, M. E., ELLIS, R. W. & PRESTON, C. D. (2006). *Change in the British Flora 1987–2004*, Botanical Society of the British Isles, London.
CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. (1952). *Flora of the British Isles*, Cambridge University Press, Cambridge.
DEHNEN-SCHMUTZ, K. & WILLIAMSON, M. (2006). *Rhododendron ponticum* in Britain and Ireland: Social, Economic and Ecological factors in its successful invasion, *Environment and History* **12**: 325–350.
HENGEVELD, R. (1989). *Dynamics of Biological Invasions*, Clapham & Hall, London.
LACEY, W. S. (1957). The Spread of *Galinsoga parviflora* and *G. ciliata* in Britain, *Progress in the Study of the British Flora*, ed. LOUSLEY, J. E., 109–115, Botanical Society of the British Isles, London.
MURRAY, R. D. (2008). The spread of Nuthatch in *Borders Bird Report No. 24*, *2006*, Scottish Ornithologist's Club, Borders Branch, Galashiels.
PERRING, F. H. & WALTERS, S. M., eds. (1962). *Atlas of the British Flora*. Thomas Nelson & Sons, London.
PERRINS, J., FITTER, A. & WILLIAMSON, M. (1993). Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles, *Journal of Biogeography*, **20**: 33–44.
PRESTON, C. D. (1988). The spread of *Epilobium ciliatum* Raf. in the British Isles, *Watsonia* **17**: 279–288.
PRESTON, C. D., PEARMAN, D. A. & DINES, T. D. (2002). *New Atlas of the British and Irish flora*, Oxford University Press, Oxford.
PRESTON, C. D. *et al.* (2003). *The changing distribution of the flora of the United Kingdom: technical report*, Centre for Ecology and Hydrology, Huntingdon.
RICH, T. C. G. & WOODRUFF, E. R. (1990). *The BSBI Monitoring Scheme, 1987–1988.* 2 vols. Nature Conservancy Council Report no. 1265, Botanical Society of the British Isles, London.
RICH, T. C. G. & SMITH, P. A. (1996). Botanical recording, distribution maps and species frequency, *Watsonia* **21**: 155–167.
SALISBURY, E. J. (1953). A Changing Flora as shown by the Study of Weeds of Arable Land and Waste places, in *The Changing Flora of Britain*, ed. LOUSLEY, J. E., 130–139, Botanical Society of the British Isles, London.
STACE, C. A. (1991). *New Flora of the British Isles*, Cambridge University Press, Cambridge.
STACE, C. A., ELLIS, R. G., KENT, D. H. & MCCOSH, D. J. (2003). *Vice-county Census Catalogue of the Vascular Plants of Great Britain, the Isle of Man and the Channel Islands*, Botanical Society of the British Isles, London.
STEWART, A., PEARMAN, D. A. & PRESTON, C. D. (1994). *Scarce plants in Britain*, J.N.C.C., Peterborough.
WILLIAMSON, M. (1996). *Biological Invasions*, Clapham & Hall, London.
WILLIAMSON, M., PRESTON, C. D. & TELFER, M. G. (2003). *On the rates of spread of alien plants in Britain* in *Plant Invasions,* CHILD, L. *et al.,* eds., Backhuys Publishers, Leiden, The Netherlands.
WILLIAMSON, M., PYSEK, P., JAROSIK, V. & PRACH, K. (2005). On the rates and patterns of spread of alien plants in the Czech Republic, Britain and Ireland, *Ecoscience*, **12**: 424–433.

(*Accepted August 2009)*