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THE EXPANSION OF THE ALIEN MOSSES *ORTHODONTIUM LINEARE* AND *CAMPYLOPUS INTROFLEXUS* IN BRITAIN AND CONTINENTAL EUROPE

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ABSTRACT. *Orthodontium lineare* and *Campylopus introflexus* are two species originally from the Southern Hemisphere. They were introduced to Europe in the early 20th century and have since expanded over much of Western Europe. The time-course of expansion in continental Europe is mapped. The expansion phase of the two species in Britain is described as the cumulative number of vice-counties where they have been found over time. This is compared with related native species from the same environment to avoid effects of sampling intensity.

INTRODUCTION

Alien plants and especially invasive alien plants, can be a threat to biodiversity and have consequently received a much recent attention (Drake et al. 1989). Following Richardson et al. (2000), a plant is alien (a neophyte) if its presence in a given area is due to intentional or accidental introduction by humans. If it reproduces consistently and sustains populations over many life cycles without direct intervention by humans it is naturalised. Such plants often recruit offspring freely, usually close to adult plants, but do not necessarily invade natural, semi-natural or human made ecosystems. For a naturalised plant to be invasive it must produce offspring, often in large numbers, at considerable distances from parent plants, and thus have the potential to spread over a considerable area. As a rule of thumb we can say that out of 100 species introduced 10 will naturalise and one will become invasive.

There are several naturalised bryophyte species worldwide. An earlier survey (Söderström 1992) showed that there were about 22 naturalised species in Europe, only 3 of which are invasive, i.e. *Orthodontium lineare*, *Campylopus introflexus* and *Riccia rhenana*. Since then a few more species have entered Europe, and *Lophocolea semiteres* is now invasive (Stieperaere 1994). This includes only species that have their origin outside Europe. There are also species native to Europe that may be naturalised outside their original area. A good example of such a species is *Pogonatum dentatum*, a taxon that has invaded the forest region of north-western Europe (and Russia) originating from mountainous and arctic areas (Hassel 2000).

Invasions or range expansions in a geographic area, when plotted cumulatively along a time scale, usually follow a logistic curve (Hengeveld 1989). This involves a slow expansion in the beginning, when the units for dispersal are few, before an exponential phase

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where dispersal units and suitable habitat are readily available. In the last phase almost all available habitats are filled, and although dispersal units are in excess very few new establishments take place.

Campylopus introflexus and *Orthodontium lineare* are two Southern Hemisphere species that have invaded Europe. The invasions in Europe have received much attention and their expansion is so well documented that it may serve as a model of the invasion process. Both species are clearly invasive in Western Europe and at least *Campylopus introflexus* is an environmental problem in certain areas (Biermann & Daniels 1997, Meulen et al. 1987).

In this paper we summarise the spread of *Orthodontium lineare* and *Campylopus introflexus* in Europe and compare their expansion pattern in Britain to other species with varying times of appearance in the British bryoflora. We also evaluate whether it is possible to use the expansion curves to determine whether a species is introduced or, for example, overlooked.

Methods

Expansion in Europe

We map the expansion of the two species in Europe on a rather coarse scale, using earliest known reports from countries and provinces (for Austria, Czech Republic, France, Germany, Italy, Norway, Poland, Portugal, Spain and Sweden). We use both literature reports and information from various colleagues around Europe, but we have not checked herbaria for any unknown collections.

Expansion pattern in Britain

For the study of expansion patterns we take advantage of extensive British data, where bryologists have recorded species from vice-counties for over a hundred year. This is a formidable source to study phenomena such as the expansion process. The data became available with the publication of the first census catalogue in 1907 (Ingham 1907). After that, several more census catalogues were issued (i.e. Duncan 1926, Warburg 1963, Corley & Hill 1981, Blockeel & Long 1998), along with annual updates.

In order to analyse the expansion pattern of each species, we use the earliest date it was recorded from each vice-county. The cumulative number of vice-counties in which it was recorded was plotted against time (year) to obtain an expansion curve. In order to test if the pattern is due to expansion or increased bryological activity, we compare plots with those of some supposed native species known since the early days of recording. In addition we include species that have been recently described, or recently clarified taxonomically.

Vice-counties are useful since they are small enough to provide sufficient spatial resolution, and they do not vary too much in size. The method has only two problems. First, all vice-counties are not equally well investigated, especially in earlier years. However, if the vice-counties that are well studied are more or less evenly distributed, this is not a major problem. Ireland, although included in the census catalogues, was much less well known in earlier times than Britain. We have, therefore, excluded Ireland from all further analysis. Secondly, the recording procedure prefers a good recent record as a voucher over the oldest

Table 1. Summary of the biology of analysed taxa. Category of interest is the justification for inclusion in the study. Habitat is from Hill et al. (1992, 1994).

Species	Category of interest	Habitat
Orthodontium lineare	neophyte	stumps, tree bases and sometimes peat
Campylopus introflexus	neophyte	peaty soil, heathlands and ruderal ground
C. pyriformis	well known	bare, acid, sandy or peaty soil in woodland, and on heaths and moors
C. flexuosus	well known	decaying stumps and logs, peat, sandy humus, soil overlying boulders
Dicranella heteromalla	well known	woodland banks, tree bases, stumps, rotten wood, sandstone rocks
Bryum capillare	well known	trees, fences, rotten wood, rocks and soil
B. radiculosum	taxonomically clarified	mortar of walls, limestone rocks, hard calcareous earth, etc.
Plagiomnium elatum	taxonomically clarified	wet calcareous fens and flushes, beside ditches and streams
Dicranella schreberiana	increasing	bare soil of arable fields, woods and moorland
Bryum ruderale	recently described	bare soil
B. gemmiluscens	recently described	bare soil in arable and stubble fields
Dicranella staphylina	recently described	arable fields

record. It is therefore sometimes difficult to know when it was first collected in certain vice counties (especially if they are recently noticed) and we are in many cases not sure if we have the earliest record. This is not a problem with the two alien species we are investigating since they have been noticed and looked for since they were discovered. However, for newly described species, or for species that have recently been taxonomically clarified, this may be a problem.

Species examined

The species we have studied, and their occurrences, are summarized in Table 1.

Orthodontium lineare Schwaegr. originates from the southern hemisphere where it is widely distributed (Fig. 1). It was first found in Europe (Britain) in 1910 (Burrell 1940).

Campylopus introflexus (Hedw.) Brid. also originates from the southern hemisphere where it is widespread (Fig. 2). It was first found in Europe (Britain) in 1941 (Richards 1963). It has also recently established itself in western North America where it now occurs from California north to British Columbia (Frahm 1980, Taylor 1997).

Campylopus paradoxus Wils., [syn. *C. flexuosus* (Hedw.) Brid.], *C. pyriformis* (Schultz) Brid., *Dicranella heteromalla* (Hedw.) Schimp. and *Bryum capillare* Hedw. are all native to Britain and well known since the earliest days of recoding. They are chosen as they grow in similar localities as the two alien species.

Bryum radiculosum Brid. has been known from Britain since the nineteenth century but not well understood until the complex was clarified (Crundwell & Nyholm 1964), It is

Fig. 1. Known distribution of *Orthodontium lineare* in the Southern Hemisphere.

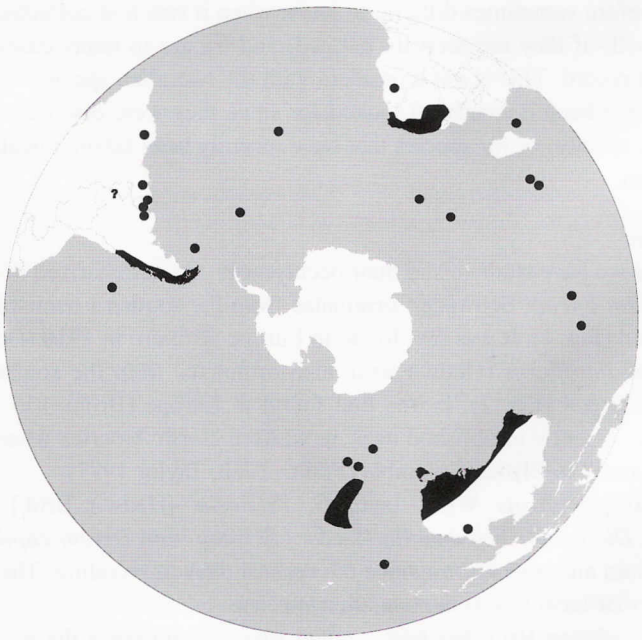

Fig. 2. Known distribution of *Campylopus introflexus* in the Southern Hemisphere.

still under-recorded in many areas (Hill et al. 1994).

Plagiomnium elatum (B. S. G.) T.Kop. is a species whose taxonomy was heavily confused in older times. It was not until the late 1960's (Koponen 1968) that it became better understood and people began to separate it from the more common *P. affine*.

Three recently described species are included, *Bryum ruderale* Crundw. & Nyh. (Crundwell & Nyholm 1964), *B. gemmiluscens* Wilcz. & Dem. (Wilczek & Demaret 1976; first reported from Britain by Smith & Whitehouse 1978) and *Dicranella staphylina* Whitehouse (Whitehouse 1969) in the analysis for comparison.

RESULTS AND DISCUSSION

Expansion in Europe

Orthodontium lineare was first found on the European continent outside Berlin in 1939 (Koppe & Koppe 1940), almost 30 year after it first was found in Britain. The distribution map (Fig. 3) shows a pattern of invasion from Western Europe (Belgium, Netherlands, and NW France) east- and north-wards. This is interesting since it was found first on the continent as far east as Berlin. This occurrence seems not to have been the source for any further spread in that region but may be the source for the large populations found early on sandstone in northern Bohemia.

Campylopus introflexus was first found on the European continent in Brittany (France) in 1954 (Størmer 1958), thirteen years after it first was found in Britain. The distribution map (Fig. 4) shows similar expansion from north-western Europe eastwards and southwards.

The apparent absence of the two species in parts of northern and north-eastern France is probably only a recording failure, and it is likely they will be found there.

It is notable that although *C. introflexus* reached Europe much later than *O. lineare* it has managed to disperse much further, and seems still to be expanding north, south and east in Europe. The rapid spread of *C. introflexus* can be explained by its high dispersal capacity, locally by fragmentation and over longer distances by small spores. *Orthodontium lineare* produces large numbers of small spores, but no asexual propagules. Thus, the local expansion may be delayed and local establishment not as easy as in *C. introflexus*. In addition *C. introflexus* occupies a greater range of available habitats than *O. lineare*. *Campylopus introflexus* is often found in more open situations and also more ruderal or heavily disturbed habitats, where spores and vegetative propagules are more easily established with less competition from other plants than in the semi-natural habitats of *O. lineare*. *Orthodontium lineare* may possibly require a long phase of acclimatisation (lag phase) before it managed to produce mature spores, which is indicated by the British expansion (see below). In Britain the lag phase of *O. lineare* was close to 30 years while for *C. introflexus* it was just above 10 years. However, this does not explain the low rate of spread after the lag phase.

Expansion pattern in Britain

Both *O. lineare* and *C. introflexus* show a typical exponential growth in number of localities (vice-counties) occupied with time (Fig. 5). The growth can be modelled using the

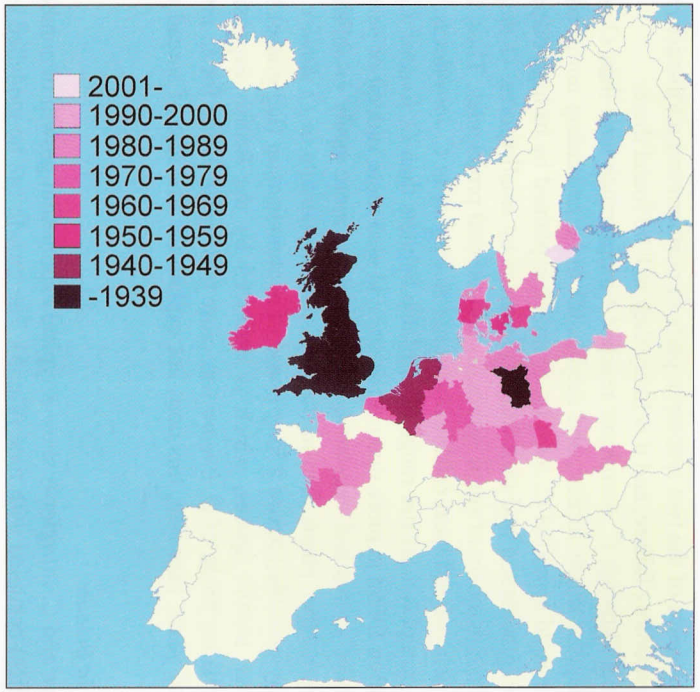

Fig. 3. Time of first report for *Orthodontium lineare* in provinces of Europe. The darker the colour, the older the first report.

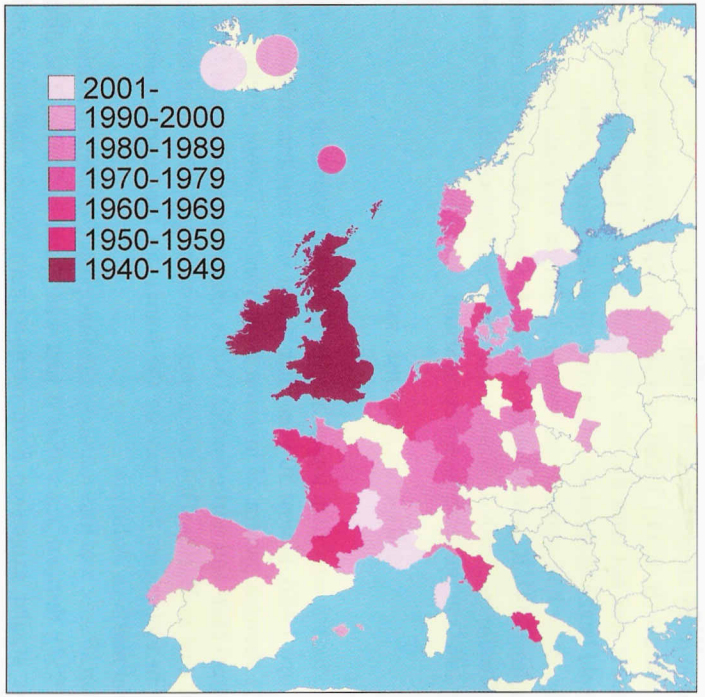

Fig. 4. Time of first report for *Campylopus introflexus* in provinces of Europe. The darker the colour, the older the first report.

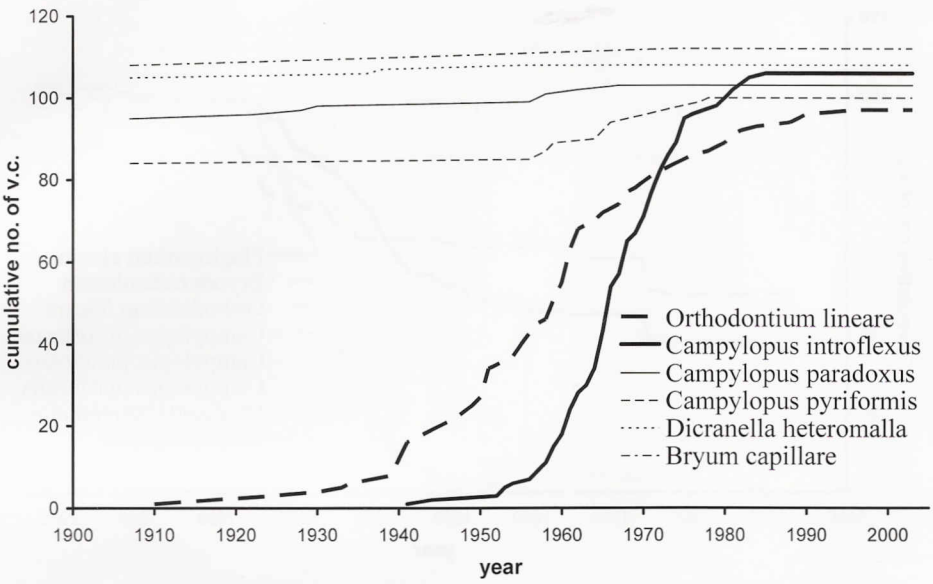

Fig. 5. Cumulative number of vice-county records of two alien (thick lines) and four native species in Britain.

Lotka-Volterra formula for exponential growth $dN/dt=rN[(K-N)/K]$. The r value describes how rapid the population growth is, the higher the r value, the more rapid the expansion. Both species have very high values, 0.10 for *O. lineare* and 0.45 for *C. introflexus*. However, in this case the r term includes not only growth but also dispersal. Assuming a radial expansion from the source, a separation of those terms would increase the growth term showing that both species are very aggressive colonisers under suitable conditions.

Campylopus introflexus seems to be a better coloniser/disperser than *O. lineare*. This may be due to its ability to quickly establish large populations once it reaches an area since it reproduces asexually by deciduous leaves. Another, not mutually exclusive explanation may be the area where the study was performed. *Campylopus introflexus* has a much more oceanic distribution pattern than *O. lineare*, both in Britain (cf. Hill et al. 1992) and Europe (Fig. 3 and 4). Further more, *C. introflexus* occurs on heaths and ruderal ground while *O. lineare* occurs on decaying wood in woodlands. Localities with decaying wood (or sandstone) are rarer in Europe and much more patchily distributed than heaths and ruderal land. Therefore, *C. introflexus* may have a larger number of suitable localities to colonize, which helps to build up local populations and increase the total number of spores that can disperse over longer distances (cf. Söderström & Herben 1997). Although *O. lineare* produces nummerous spores the output might not always be enough to overcome larger dispersal distances (cf. Hedenäs et al. 1989) and expansion will be slower.

Is the observed pattern of increase just an effect of increased activity of bryologists around Britain? If so, native species should also show a similar increase. We sampled two

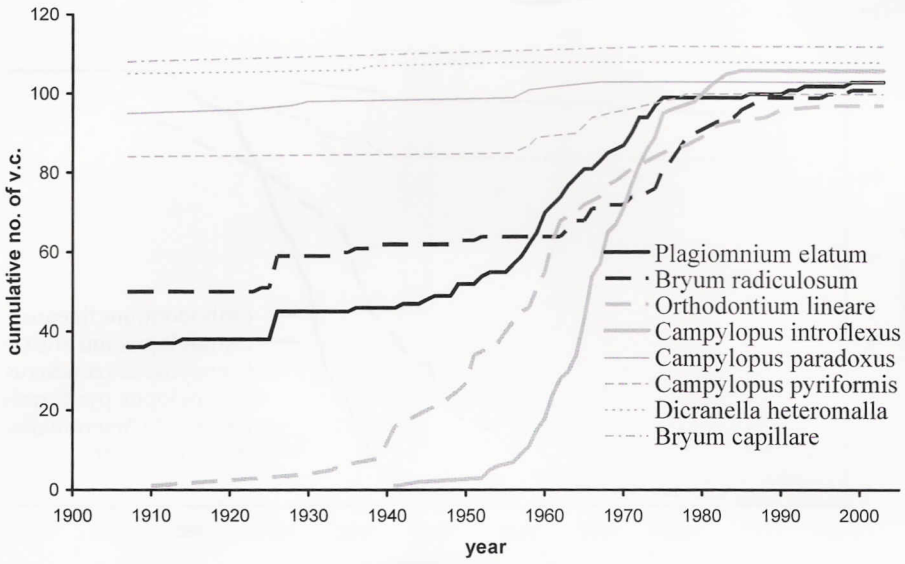

Fig. 6. Cumulative number of vice-county records for two species recently clarified taxonomically (black lines) compared with two alien and four native species (grey lines) in Britain.

species with similar habitat preferences to *O. lineare* (*Dicranella heteromalla* and *Bryum capillare*), and two species with similar preferences to *C. introflexus* (*C. paradoxus* and *C. pyriformis*). All four species are well-known since the start of recording and they were already known from almost all vice counties in 1907 (Fig. 5). It is thus clear that the expansion cannot be completely explained by increased activity. However, species may be overlooked due to taxonomic uncertainty or confusion. Two species included that recently have been clarified are *Plagiomnium elatum* and *Bryum radiculosum*. They show a more or less exponential increase shortly after their taxonomic status was clarified (Fig. 6), but they were known from (collected in) a fair number of vice counties already before that. The older identifications of *B. radiculosum* are mostly correct, so its pattern may be explained by increased activity and that bryologists have learned to recognize it. *Plagiomnium elatum* was earlier mainly recognised as a variety of *P. affine* and the pattern is probably due to lower recognition of, and search for, varieties than for species.

It is interesting to compare the pattern of *O. lineare* and *C. introflexus* with newly described species. Three such species are *Bryum ruderale, B. gemmilucens* and *Dicranella staphylina* (Fig. 7). If those species are native but overlooked there should be older collections in herbaria. For the two *Bryum* species, there are some collections older than 1907. Except for the few old collections the expansion curve of *B. ruderale* is very similar to that of *O. lineare*, with a long lag phase before the exponential increase. However, the increase is rapid shortly after the species were described. This may be because the recording procedure is not targeting the oldest record and thus older specimens may exist. Another explanation is that when a species gets attention, bryologists tend to look more for them and thus

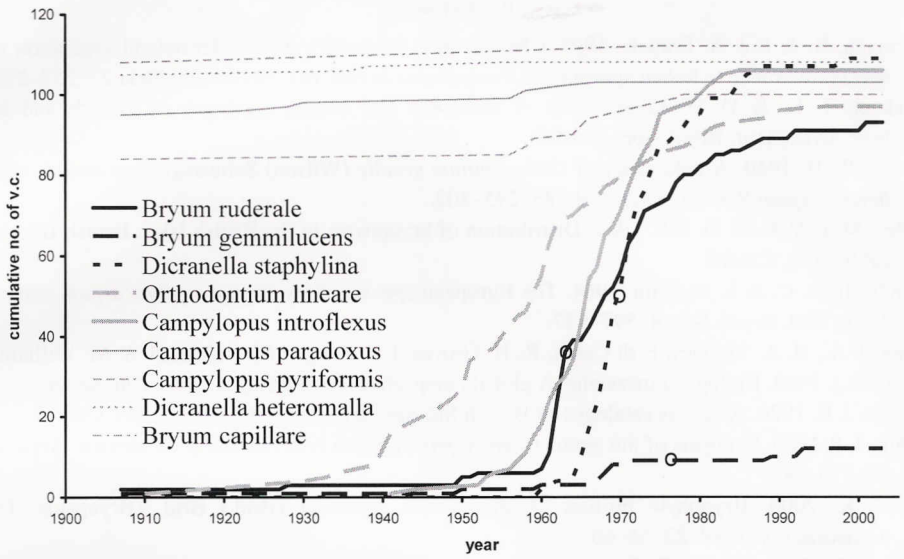

Fig. 7. Cumulative number of vice-county records for three recently described species (black lines) compared with two alien and four native species (grey lines) in Britain. The circle on the line is the year of description.

more often find them.

We could not find any report of *Dicranella staphylina* from before 1960. The increase of this species is even more rapid than for *C. introflexus*. Is it an alien species? Both arguments for and against can be found. An argument for being alien is that it does not produce sporophytes, the closely related *Dicranella varia* (dioecious and occupies similar habitats as *D. staphylina*) is commonly found with sporophytes. Maybe the conditions for sexual reproduction in *D. staphylina* are not right and its origin should be sought in areas with some other climate (cf. *Henediella macrophylla*; Söderström 1992). Lack of sexual reproduction can also be used as an argument against it being alien. All clearly invasive species in Europe produce large numbers of small, easily dispersed, spores. The main means of dispersal for *D. staphylina* is tubers, and these are not easily transported over large distances by wind. It is therefore unlikely that the species should show such a rapid increase. Instead, increased interest for bryophytes of arable land, and ability to recognise the species when sterile are more probable explanations.

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