Invaders on the move: parasitism in the sexual galls of four alien gall wasps in Britain (Hymenoptera: Cynipidae)

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Four alien, host-alternating cynipid gall wasps are established in the British Isles: *Andricus kollari*, *A. lignicola*, *A. quercuscalicis* and *A. corruptrix*. Their current distributions divide Britain into four zones; all four invaders are present in the south and south-east of Britain, whereas only *A. kollari* is present in the far north of Scotland. The rank order, according to how far north the distributions of the four invading cynipid species reach, is: *A. corruptrix* → *A. quercuscalicis* → *A. lignicola* → *A. kollari*.

The life cycles of all four cynipid species involve a sexual generation in spring on *Quercus cerris*, and an agamic generation in autumn on *Q. robur*. Here we studied the parasitoid attack by four pteromalid species on the sexual generations of the invaders. We collected and reared the galls of all four species at eight sites from the south to the north of the country (two sites per zone). The geographical locations of the sites reflect the invasion history and thus the residence time of the alien species in the four zones. At each site we measured the densities of all host galls on *Q. cerris* and of both obligatory host-tree species. We also took a series of measures, such as host-tree density and mean host-tree size, to further characterize the tree stands. These measures are referred to as local parameters.

Host densities varied between sites and between years. In *A. kollari*, galling rates were highest in the middle of the country (zone 2) in 1994, whereas in 1995 they increased from the south to the north. In *A. lignicola*, galling rates in both years were lowest at the sites in zone 3 (closest to its distribution boundary). In *A. quercuscalicis*, galling rates were found to be lowest at the site most to the north-west in both years, again the one furthest away from the area where this species was first recorded.

Mortality caused by parasitoid attack differed from less than 10% to as high as 70% and varied between host species, sites and years. In four out of six cases the historical/regional variables (north/south and east/west) correlated significantly with parasitoid attack rates that were characteristically lowest at sites close to the distribution boundaries. Of the local factors, we found parasitoid attack rates correlated negatively in one case with host density, whereas they correlated positively in four cases with the density of alternative hosts of the parasitoids. In one of the models the local density of *Q. cerris* trees correlated negatively with parasitoid attack on *A. quercuscalicis*. For all three host species the terms retained in the minimal adequate models obtained for 1994 and 1995 differed, which might indicate that these communities of native parasitoids and invading host have not yet settled in any definite structure.

Keywords: cynipid gall wasps; community ecology; parasitoids; biological invasion; regional/historical processes; local/contemporary processes

1. INTRODUCTION

Biological invasions have raised considerable interest as ecological phenomena, but they have also been interpreted as large-scale natural experiments (Elton 1958; Diamond 1986). Native communities are disturbed by the arrival of an alien species. After the invasion (a regional process), the alien might then interact with native species through local processes, such as competition, predation or, here, host–parasitoid interactions (Simberloff 1991; Williamson 1996). The importance of both regional/historical and local/contemporary processes for the

structure of communities has been pointed out repeatedly (MacArthur 1972; Ricklefs 1987). By studying parasitoid attack on four alien gall wasps in Britain, we try to assess the relative importance of regional/historical and local/contemporary processes for the community structure of this species complex.

The native cynipid fauna on English oak (*Quercus robur*) and sessile oak (*Q. petraea*) in Great Britain has been invaded over the last 150 years by four alien, host-alternating gall wasps native to south-eastern Europe: *Andricus kollari*, *A. lignicola*, *A. quercuscalicis* and *A. corruptrix* (Claridge 1962; Quinlan 1974; Darlington 1974; Csóka *et al.* 1998). A prerequisite for the success of all four invasions was the introduction of the Turkey oak (*Quercus cerris*) to Britain, which is the second obligatory host-tree for all four species (Mitchell 1974). Most recently, another

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new cynipid species (*Aphelonyx cerricola*), a species that has only one generation per year and is specialized to induce galls on *Q. cerris*, has been recorded in Britain (Crawley 1997). However, this species is known only from one location in the south of England and is not part of this study.

The recruitment of natural enemies to invading species has received a great deal of attention (Cornell & Hawkins 1993, 1994); in particular, the recruitment of parasitoid and inquiline species to the galls of *A. quercuscalicis* has been studied for more than 20 years (Collins *et al.* 1983; Hails *et al.* 1990; Hails & Crawley 1992; Schönrogge *et al.* 1995, 1996a,b; Stone *et al.* 1995). The tiny and structurally relatively simple galls of the sexual generation of *A. quercuscalicis* were already attacked by native parasitoids when the first studies began in the late 1970s (ca. 35 years after its arrival). The four parasitoid species that attack these galls in Britain have also been reared from galls collected in the native range, where an additional nine parasitoid species have been recorded (Stone *et al.* 1995). Two facts about the parasitoid attack in these galls in Britain were particularly remarkable: (i) more than 90% of the emerging parasitoids were male; and (ii) total parasitism rates (summed over all parasitoid species) changed very little between years ($30\% \pm 5\%$; Hails 1989; Hails & Crawley 1991). During the 1980s, the first parasitoid species had been reared from the galls of the agamic generation of *A. quercuscalicis*, which were previously found to be free from parasitoids and inquilines (Hails *et al.* 1990). Species richness in the parasitoid community increased slowly until, in the early 1990s, inquilines were recruited to the galls. Subsequently, parasitoid species richness, and parasitoid and inquiline abundance, have both increased rapidly (Hails *et al.* 1990; Schönrogge *et al.* 1996a). Two geographical patterns in parasitoid recruitment could be identified. First, within Britain the increase in parasitoid and inquiline abundance appears to be consistent with the invasion route. Second, following the parasitoid and inquiline community structure throughout the invaded range in Europe, a strong convergence was detected towards the species composition found in the agamic galls of *A. quercuscalicis* in the native range (Hails *et al.* 1990; Stone & Sunnucks 1993; Schönrogge *et al.* 1995, 1996a).

Although the invasions of *Andricus kollari*, *A. lignicola* and *A. corruptrix* have received less attention than that of *A. quercuscalicis*, we studied parasitoid attack in the sexual galls of all four invading species. In contrast to previous studies that followed the invasion route back to the native range of the alien species, we studied them and their associated parasitoid species from the area in Britain where they entered the country towards their current distribution boundaries.

The sexual generations of all four alien species in Britain are attacked by four pteromalid parasitoid species: *Mesopolobus fuscipes*, *M. xanthocerus*, *M. tibialis* and *M. dubius*. Of these four species, *M. fuscipes* is the most abundant, and in northern areas, the only parasitoid species to attack the alien gall wasps on *Q. cerris* (Schönrogge *et al.* 1999). The attack rates of each individual parasitoid species are discussed by Schönrogge *et al.* (1998). They are all univoltine except *M. tibialis* (Askew 1961b). Recent studies have shown that the four *Mesopolobus* species switched to the new alien hosts, rather

Figure 1. The geographical location of the eight sample sites (site numbers are given in parentheses). The thick lines indicate the boundaries of the four zones according to the current distribution of the four invading gall wasp species (see text).

than extended their host ranges (K. Schönrogge, unpublished data). Thus the four invading cynipid species and their associated parasitoids represent a relatively closed community.

We use this well-defined community to investigate the importance of local/contemporary versus regional/historical factors on the host–parasitoid interactions. Historical factors are represented by the geographic distribution of the gall wasps and the parasitoid attack rates. Local factors are the galling rates of the different species and a series of measures taken to characterize the tree stands at each site. We ask the questions: (i) how the invasion histories (i.e. their residence times) of the alien gall wasps might affect the parasitoid attack rates; and (ii) what is the relative importance of the invasion histories for parasitoid attack rates as opposed to local processes?

2. METHODS

(a) Selection of sites and trees

Previous work established the geographical distribution within the British Isles of four invading cynipid species, *A. kollari*, *A. lignicola*, *A. quercuscalicis* and *A. corruptrix*, and four geographical zones were defined, based on the number of alien species present (Schönrogge *et al.* 1994, 1996a; figure 1). All four species were recorded in south-eastern England (zone 1); *A. corruptrix* was absent from zones 2–4; *A. quercuscalicis* was absent from zones 3 and 4; whereas *A. kollari* was the only invading species in zone 4 in northern Scotland.

Within each of the four zones, two sites were chosen using the following criteria: (i) the sites had to be at least 45 km apart (thus assuming that there was no or little interaction between the populations we sampled); (ii) both host-oak species, *Quercus cerris* and *Q. robur*, had to be present; and (iii) the oak stands had to be sufficiently large to allow the selection of six trees for each host-oak species (see figure 1).

In 1994, six trees of each oak species were selected at random from marked cohorts of suitable trees, and in 1995 a further six trees of each host species were added to the samples (only seven Turkey oaks were recorded at the northernmost site, Dunrobin Castle in Sutherland).

A square of at least 100 m × 100 m was chosen at each site and, within it, the number of individuals of both species of oak was recorded. The girth at breast height (GBH) was measured from each tree within the area. The tree density was later standardized and expressed as numbers per 100 m².

(b) Randomized sampling of shoots

Samples of 30 branches in 1994, and 15 branches in 1995, were taken from various aspects and heights of each of the selected sample-trees. A 6-m pole-pruner allowed a reach of ca. 8 m. A branch is defined as four years of growth, as identified by the number of terminal bud scars. Six shoots (defined as last year's growth), were then chosen at random from every branch and the number of galls of each cynipid species were counted. The galls of the spring generation of the invading cynipid species on *Q. cerris* are very small (<4 mm) and concealed within the buds. Thus *Q. cerris* shoots were taken back to the laboratory for subsequent dissection.

(c) Gall collection and rearing

Samples were taken twice each season to accommodate the different phenologies of the oak and cynipid species, and to allow collections of the galls under the best possible conditions for rearing. The first samples were taken from *Q. cerris* trees by mid-April before bud burst had occurred. A second sample was taken at the beginning of May when leaves, catkins and flowers were fully expanded.

Buds containing the galls of *A. kollari*, *A. lignicola* and *A. corruptrix* were removed from the shoot and kept individually in 2-ml glass vials. To rear the galls of *A. quercuscalicis*, catkins were incubated individually in the same kind of glass vial. All rearings were kept in an outdoor insectary where we collected all emerging adults weekly, which were then identified.

(d) Statistics

Total parasitoid attack rates in the sexual galls of *Andricus kollari*, *A. lignicola* and *A. quercuscalicis* were analysed separately for the years 1994 and 1995 using general linear models with a binomial error distribution and logit link functions. We used the site means of the response and explanatory variables to avoid pseudoreplication for the analyses on zone level. The explanatory variables fall into two categories (variable names used are in bold type).

1. Regional/historical: (i) **north–south** distribution is a categorical variable with factor levels according to the number of zones where the species were present (distances between sites in different zones are so far that this variable also represents different residence times); (ii) **east–west** distribution is a two-level factor.

2. Local/contemporary: (i) **density(species)** is the mean number of galls per shoot of either of the cynipid species on *Quercus cerris*; (ii) **bud galler** is the density (mean galls per shoot) of those cynipid species that share buds as the site of gall induction (i.e. *A. kollari*, *A. lignicola* and *A. corruptrix*); (iii) **total** is the mean gall density on Turkey oak of all four invading species; (iv) *Q. cerris* and *Q. robur* are the relative densities per 100 m² at each site of the two obligate host-tree species of the alien cynipid species; (v) **GBH** is a measure of the mean tree size of English and Turkey oak at each site.

All variables were fitted separately and ranked according to the amount of deviance they explained. The maximum number of terms was then fitted (depending on the available number of degrees of freedom), and assessed for significance by successive elimination (test statistic was a χ^2 -test). After arriving at a minimum model, the remaining explanatory variables, squared terms (to test for nonlinearity) and first-order interactions were fitted and tested for significance. Model criticism on the resulting minimum adequate model was done as described by Crawley (1993).

3. RESULTS

(a) The sites

The eight sites were selected to represent the four zones shown in figure 1. All but Beauly were managed park or common lands. The trees at Beauly were planted along a main road with little undergrowth but hedges between them. The stand at Beauly was made up of large trees that were very homogeneous in size (table 1).

At the four southern sites (site nos 1–4), the introduced oak species *Q. cerris* was naturally recruiting and tree size was variable (table 1). This was particularly apparent at site 3 (Tatton Park), where under large trees an undergrowth of *Q. cerris* of almost bushy appearance led to the highest relative density for this species (table 1). At site 5 (Erskine Bridge) we found seedlings of *Q. cerris*. However, the trees appeared to fall into two size cohorts, and it seems likely that those trees were planted while seedlings might be regularly removed. North of site 5 there was no sign of any natural recruitment by *Q. cerris*.

With the exceptions of site 3 and site 6 (Tatton Park and Falkland), the native oak species *Quercus petraea* and *Q. robur* showed a higher relative density than *Q. cerris*. In contrast to the introduced oak species, we found signs for natural recruitment at all sites. Recruitment was reduced at the most northern sites, leading again to a more homogeneous size distribution due to large-scale planting (table 1).

(b) Gallling rates

The gallling rates of the longest-established alien species, *A. kollari*, varied by an order of magnitude between sites and years (table 2). The change in density was particularly pronounced at the most northern site where only a quarter of shoots examined in 1994 had a bud that was galled, whereas in 1995 every shoot had at least one gall (see also site 6 and site 7; table 2). The gallling rates of the later arrivals, *A. lignicola*, *A. quercuscalicis* and *A. corruptrix*, were more consistent between years, although they still changed by a factor of two (e.g. *A. lignicola* at site 1 and *A. quercuscalicis* at

Table 1. *Characteristics of the oak stands at the eight sample sites*

(The mean and s.d. of the girth at breast height (GBH) are given as measures of tree size in each stand. The variance-to-mean ratio is a measure of homogeneity of the tree size distribution (the larger the value the more heterogeneous the size distribution). *Quercus* spp. include the two native oak species, *Q. robur* and *Q. petraea*, as well as the hybrid species *Q. × rosacea*.)

site numbers and names	species	<i>n</i>	trees per 100 m ²	mean GBH (cm)	s.d. GBH (cm)	variance/ mean ratio
1	<i>Q. spp.</i>	17	0.86	76.41	42.68	23.84
Silwood Park	<i>Q. cerris</i>	2	0.16	81.50	55.86	38.29
2	<i>Q. spp.</i>	33	7.40	43.58	16.76	6.45
Puttenham Common	<i>Q. cerris</i>	5	1.79	45.80	22.23	10.79
3	<i>Q. spp.</i>	4	1.27	136.75	133.88	131.07
Tatton Park	<i>Q. cerris</i>	85	12.86	21.81	43.17	85.45
4	<i>Q. spp.</i>	21	2.07	51.76	44.50	38.26
Rufford Park	<i>Q. cerris</i>	12	2.01	48.50	30.91	19.69
5	<i>Q. spp.</i>	32	0.29	94.98	90.93	87.05
Erskine	<i>Q. cerris</i>	11	0.12	91.30	89.31	87.36
6	<i>Q. spp.</i>	13	0.60	111.00	96.52	83.93
Falkland	<i>Q. cerris</i>	14	0.65	53.23	75.75	107.79
7	<i>Q. spp.</i>	13	0.14	270.83	60.08	13.33
Beaulay	<i>Q. cerris</i>	11	0.09	276.50	27.39	2.71
8	<i>Q. spp.</i>	10	0.01	166.56	79.52	37.97
Dunrobin Castle	<i>Q. cerris</i>	8	0.01	192.71	46.07	11.02

Table 2. *Galling rates on the trees of Quercus cerris*

(All buds on the shoots were dissected for the bud galls of *Andricus kollari*, *A. lignicola* and *A. corruptrix*, whereas the catkins on those shoots were examined for galls of *A. quercuscalicis*. The category 'bud gallers' gives the galling rates for the three species together that share buds as the oviposition site, whereas 'total' also includes the galls of the catkin galler *Andricus quercuscalicis*.)

site no.	number of shoots examined	galling rates (galls per shoot)					total
		<i>Andricus kollari</i>	<i>Andricus lignicola</i>	<i>Andricus quercuscalicis</i>	<i>Andricus corruptrix</i>	bud gallers	
1994							
1	895	0.18	0.37	0.54	0.12	0.67	1.20
2	1027	0.16	0.20	0.19	0.18	0.55	0.74
3	1025	0.23	0.16	0.04	—	0.39	0.43
4	1028	0.26	0.32	0.66	—	0.58	1.25
5	832	0.28	0.24	—	—	0.52	0.52
6	624	0.03	0.14	—	—	0.17	0.17
7	1040	0.08	—	—	—	0.08	0.08
8	691	0.23	—	—	—	0.23	0.23
1995							
1	1085	0.05	0.63	0.45	0.12	0.79	1.24
2	1093	0.04	0.20	1.16	0.14	0.38	1.54
3	1049	0.14	0.12	0.14	—	0.26	0.40
4	1043	0.07	0.28	0.84	—	0.35	1.19
5	815	0.07	0.14	—	—	0.21	0.21
6	969	0.12	0.18	—	—	0.30	0.30
7	865	0.40	—	—	—	0.40	0.40
8	615	1.23	—	—	—	1.23	1.23

site 3; table 2). *Q. cerris* trees at site 2 (Puttenham Common) suffered during a strong air frost in early May 1994. Although the bud gallers were not affected, the frost killed most of the catkins on the trees and with them the galls of *A. quercuscalicis*. In fact, of the marked trees for the randomized sampling, only one was bearing catkins without frost damage.

For all species and in both years, the sites from zone 1 were between the high-density sites. However, gall density at individual sites further north reached the same or even higher levels of gall densities (table 2). There was no geographical gradient in gall density that could be related to the invasion history of the alien species.

Figure 2. Total parasitism rates in the sexual galls of (a) *Andricus kollari*, (b) *A. lignicola*, (c) *A. quercuscalicis* and (d) *A. corruptrix* in the seasons 1994 and 1995. The numbers (*n*) above the bars give the number of galls from which the parasitoids were reared.

Table 3. *Statistical modelling using parasitism rates in the sexual galls of Andricus kollari, A. lignicola and A. quercuscalicis in the years 1994 and 1995 as response variables (GLIM, binomial errors, logit link)*

(All parameters included in the table caused a significant change in deviance ($p < 0.05$) when deleted from the minimal adequate model. Parameter estimates and standard errors are in logits.)

species	1994				1995			
	explanatory variables	parameter estimates	s.e.	per cent deviance explained	explanatory variables	parameter estimates	s.e.	per cent deviance explained
<i>Andricus kollari</i>	east–west _(east)	0.95	0.42	57.75	north–south _(zone 1)	–0.38	0.49	78.70
	east–west _(west)	–0.28	0.35		north–south _(zone 2)	–0.45	0.50	
	density _(Andricus kollari)	–4.14	2.12	22.30	north–south _(zone 3)	–1.31	0.48	
	total	1.90	0.46	15.30	north–south _(zone 4)	–3.39	0.50	
					bud gallers	0.79	0.44	8.39
<i>Andricus lignicola</i>	density _(Andricus kollari)	2.93	1.91	65.06	north–south _(zone 1)	–0.60	0.21	65.69
					north–south _(zone 2)	–0.33	0.26	
					north–south _(zone 3)	–1.47	0.37	
<i>Andricus quercuscalicis</i>	north–south _(zone 1)	–0.85	0.07	90.71	total	–2.49	0.41	40.02
	north–south _(zone 2)	–2.19	0.17		<i>Q. cerris</i>	–0.11	0.03	13.79
	east–west _(east)	–1.12	0.06	11.20				
	east–west _(west)	–1.58	0.18					

(c) Parasitism in the sexual galls

The total parasitism rates in the sexual galls of the four alien species in 1994 and 1995 are shown in figure 2*a–d*. For all four species, rates of total parasitism were variable between sites and between years. In contrast to the galling rates of *A. kollari*, which all decreased from 1994 to 1995 at sites 1–5, parasitism rates in the galls increased at two sites and decreased at the other three sites (table 2 and figure 2*a*). At sites 6–8, parasitism rates decreased from the low-gall-density year 1994 to the high-gall-density year in 1995, most markedly so at site 7 where parasitism rates dropped from more than 70% to less than 10% (figure 2*a*). Of all the parameters we measured, the geographical variables north–south and east–west explained most of the deviance in both years. However, in 1994 there was an east–west divide, whereas in 1995 parasitism rates decreased from the south to the north (mean mortalities by parasitism in the zones 1–4 were, respectively, 40.6%, 38.9%, 21.2% and 3.3%; figure 2*a* and table 3). Mortality by parasitoid attack also correlated negatively with the density of *A. kollari* galls and positively with total gall density (in 1994) and the density of all bud gallers (in 1995; table 3).

Parasitism rates in the galls of *A. lignicola* increased from site 1 to site 4, only to drop off sharply at the sites further north (sites 6 and 7; figure 2*b*). In 1994, mortality by parasitoid attack in *A. lignicola* correlated positively with the density of *A. kollari* galls (table 3), whereas for 1995 the three-level factor north–south was the only parameter to be retained in the model (table 3). In contrast to parasitism rates in the galls of *A. kollari*, attack rates in the galls of *A. lignicola* were highest in zone 2 (41.8%) and lower south and north of it (35.4% and 18.7%, respectively; figure 2*b* and table 3).

The analyses of parasitism rates in the galls of *A. quercuscalicis* resulted in completely different minimal adequate models for 1994 and 1995. The two geographical variables north–south and east–west were the only terms to be retained in the model for 1994, with attack rates being the lowest in the north and west (figure 2*c* and table 3). In contrast, parasitism rates correlated negatively with the total gall density and the density of *Q. cerris* trees at the sites in 1995 (table 3). The site furthest to the north and west in the range of *A. quercuscalicis*, Tatton Park, has also the highest relative density of *Q. cerris* trees, so that there is a strong correlation between both terms (table 1). However, in this model the relative density of the host-tree explained a larger amount of the deviance than the geographical variables.

4. DISCUSSION

The geographical distributions of the four alien gall wasps, *Andricus kollari*, *A. lignicola*, *A. quercuscalicis* and *A. corruptrix*, reflect their invasion history. All four species spread from the south and south-east of England to the north and into Scotland so that the different zones in this study also represent different periods of residence time for the invaders. Here we found that the geographical variables explained the largest amount of deviance in the parasitoid attack rates. However, the terms for the minimum adequate models for the same host species differed considerably between years. This might suggest that the parasitoid community associated with the invading species is not yet well structured.

The geographical variables in our models represent the invasion history and the residence times of the four alien cynipid species. Local factors were represented as

measures that characterize the stands of host-trees: (i) relative host-tree density, (ii) mean tree size and (iii) the distribution of tree size. Parallel to this study we also investigated parasitism in the native cynipid hosts at the eight sites (K. Schönrogge, unpublished data). From those data we could establish that the alien cynipid species on *Q. cerris* and their associated parasitoid species are a relatively closed community. The densities of the alien cynipid species represent the availability of alternative hosts for the parasitoid species discussed here (only one of the four parasitoid species involved, *Mesopolobus tibialis*, was also reared in comparatively small numbers from native cynipid galls).

The geographical location from the south to the north was retained in three of the six models and parasitoid attack rates were always lowest in the zone closest to the distribution boundaries. In two models, the factor east–west was retained and parasitism rates were lower in the western side of the country. In all of these cases the distribution of parasitoid attack rates appeared to be consistent with the invasion routes from the south-east towards the north and west. Comparisons between years, however, also showed a large degree of variation in parasitoid attack rates at each of the sites. The most pronounced decreases in attack rates were observed for *A. kollari* from 1994 to 1995 at the most northern sites, whereas galling rates increased over the same period more than tenfold at site 7 and twofold at site 8. It has been suggested that the change in gall density is caused by the complex life cycle of *A. kollari*, which appears to have a two-year life cycle in the north of Scotland (Schönrogge *et al.* 1999). The low attack rates in high-density years would then be caused by the satiation of the parasitoid populations. This seems to be further supported by the negative correlation between *A. kollari* gall density and parasitoid attack rate in 1994. However, mortality in *A. kollari* galls due to parasitoid attack also correlated positively with the total gall densities in 1994 and the bud gall densities on *Q. cerris* in 1995. Similarly, parasitoid attack in *A. lignicola* galls correlated positively with the density of *A. kollari* galls in 1994.

The galls of the three bud-galling species on *Q. cerris* are very similar in their morphologies and phenologies, both characteristics of galls that are thought to have a strong determining effect on the parasitoid community structure associated with galls (Askew 1961a; Schönrogge *et al.* 1995). The vast diversity in the morphologies of cynipid galls could well be the reason that large numbers of cynipid species can coexist, while supporting large associations of polyphagous parasitoid species (Askew 1961a; Plantard *et al.* 1997; Stone & Cook 1998). However, because the sexual galls, and particularly the bud galls, of the alien species on *Q. cerris* are so very similar, they might well be interacting indirectly through shared parasitoid species. To our knowledge, this is the first time that evidence for the possibility of interspecific competition for parasitoid-free space between cynipid gall wasps has been produced (Jeffries & Lawton 1984). The relative importance of cynipid–host-plant and cynipid–parasitoid interactions for the gall wasp populations cannot be assessed from the data presented here, and would make an interesting subject for future research.

A. quercuscalicis is the best-studied invader of the four alien species. In 1994, we found both geographical factors to explain the largest amount of the deviance in parasitoid attack rates on the catkin galls of this species. The zone means reflect the invasion route of *A. quercuscalicis*, and this species suffered the lowest parasitoid attack rates at Tatton Park (site 3) in the north and west of its range. The total density of galls on *Q. cerris* and the relative density of this host-tree species were the only terms retained in the model for 1995. In contrast to *A. kollari* and *A. lignicola*, parasitism rates in the galls of *A. quercuscalicis* were negatively correlated with the overall gall density on *Q. cerris*. The negative correlation of parasitoid attack rates with the relative density of *Q. cerris* was the only variable concerning the tree stands at the sites that was retained in any of the models. However, this correlation is strongly affected by the exceptionally high density of *Q. cerris* trees at Tatton Park (site 3), where *A. quercuscalicis* arrived most recently, and where galling rates were lowest. In this case, residence time (a historical factor), gall density and host-tree density (local factors) are correlated with each other and do not allow an unambiguous interpretation of this correlation.

In summary, we found significant patterns in the geographical distribution of parasitoid attack rates in three alien gall wasps on *Q. cerris*. With parasitoid attack being the lowest to the distribution boundaries, they reflect the invasion histories of the alien species even, as in case of *A. kollari*, after *ca.* 150 years. However, parasitoid attack was also affected by local factors, namely the gall densities on *Q. cerris*. Although there appear to be intricate interactions between the invading species through their shared parasitoids, we found very little evidence that host–plant characteristics affect parasitoid attack rates.

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