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Range expansion and enemy recruitment by eight alien

gallwasp species in Britain

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24 **Abstract**

25   1. Biological invasions involving continuous range expansion differ from discontinuous

26   introductions in that invaded and native ranges remain connected, potentially allowing

27   pursuit of range expanding species by their natural enemies. The establishment in Britain of

28   eight alien herbivorous gallwasps (Hymenoptera: Cynipinae) provides a rare opportunity to

29   study continuous range expansion and natural enemy recruitment in a guild of related and

30   ecologically similar species.

31   2. Four aliens (*Andricus kollari, A. quercuscalicis, A. lignicolus* and *A. corruptrix*) reached the

32   UK before 1990, while four more recent invaders (*A. aries, A. grossulariae, A. lucidus* and

33   *Aphelonyx cerricola*) reached Britain by 2000. We provide the first parasitoid records for the

34   recent invaders, update community development for the earlier set, and use dates of first

35   record to estimate rates of spread for all 8 species.

36   3. While the recent invaders are restricted to southern and eastern England, three of the early

37   invaders have reached northern Scotland. From their origins in southern England, invading

38   gallwasps have expanded their distributions across the UK at mean rates ranging from 1.4

39   km/year to >20 km/year. Variation in range expansion rate was not related to life-history

40   differences, including voltinism or host oak association.

41   4. All species have recruited native parasitoid enemies since their arrival, and we found no

42   evidence of pursuit by non-native natural enemies from continental Europe. Our results

43   suggest that over timescales predicted for rapid climate change, herbivore/parasitoid

44   communities are unlikely to expand their range as sets of interacting species. Rather, we

45   expect host range expansions to trigger local reassembly of communities.

46

Introduction

Anthropogenic introductions of species to regions discontinuous with their native range are widely recognised as one of the five main global threats to native biodiversity (Sakai et al., 2001; Pimental, 2002; Tylianakis et al., 2008; Westphal et al., 2008). Growing numbers of studies, however, document range expansion into areas continuous with species' native ranges - an alternative mode of invasion predicted to occur increasingly in response to climate change (e.g. Walther et al., 2002; Parmesan & Yohe, 2003; le Roux & McGeoch, 2008). The ecological impacts of continuous range expansion are likely to differ from those associated with discontinuous range expansion for two reasons. First, while discontinuous range expansion often allows invading species to escape sympatric natural enemies (Jeffries & Lawton, 1984; Keane & Crawley, 2002), continuous range expansion potentially allows pursuit by such enemies, and hence multitrophic impacts on native communities (Hayward & Stone 2006, Nicholls et al. 2010a,b). Second, in comparison to long-range invasions, continuous range expansion is more likely to bring into contact species that were sympatric in the past and so retain the ability to interact. Such 'ecological familiarity' predicts (i) rapid assembly of an enemy community centred on the invader and (ii) reduced destabilising impacts of the invader on native communities (Hayward & Stone 2006; Stone et al., 2008; Nicholls *et al*. 2010a,b).

There are very few long term studies of community development centred on multiple, trophically-equivalent invaders. One example is provided by work on insect communities associated with cynipid galls (Hymenoptera; Cynipinae) on European oaks (*Quercus*), comprising the gall inducers, herbivorous non-galling inquiline wasps (also Cynipinae) and chalcidoid parasitoids (Askew 1961; Stone et al., 2002; Stone & Schönrogge, 2003; Hayward & Stone, 2005; Bailey et al., 2009; Ács et al. 2010). Because the species involved are only found in cynipid galls, the system is ecologically closed and can meaningfully be studied in isolation. These communities have become a model system in invasion ecology because multiple gallwasp species have expanded their ranges

73 following human dispersal into northern Europe of two oak species - Turkey oak (*Quercus cerris*),

74 and holm oak (*Quercus ilex*). Native to southern Europe, both have been widely planted across

75 much of northern Europe over the last 500 years, and are now naturalised as far as Scotland and

76 Scandinavia (Stone & Sunnucks, 1993; Walker et al., 2002; Hayward & Stone, 2005; for UK range

77 maps of all oaks discussed in this paper, see Walker *et al*., 2002 and BSBI, 2011). This range

78 expansion has triggered multiple range expansions by two groups of oak gallwasps: specialist

79 feeders only on *Q. cerris* or *Q. ilex*, and other species whose lifecycles involve obligate host

80 alternation between a sexual generation on *Q. cerris* and an asexual generation on native oaks,

81 particularly *Quercus petraea* and *Quercus robur*.

82

83   Four host-alternating gallwasps (here termed the Early aliens) reached Britain between 1834

84 and 1974 (Table 1, Fig. S1). Galls of *Andricus kollari* (Smith, 1854) were deliberately imported

85 from the eastern Mediterranean as a source of tannin in the 1830's (Walker et al., 2002; Stone et al.,

86 2007). From initial introductions in the Exe Valley, Devon (1834), *A. kollari* reached central

87 Scotland within 40 years (Table 1; Walker et al., 2002) and the Inner Hebrides by the 1940's

88 (Wormell, 1982). *Andricus quercuscalicis* (Claridge, 1962), *Andricus lignicolus* (Hutchinson, 1974;

89 Quinlan, 1974) and *Andricus corruptrix* (Hutchinson, 1974) each expanded their distributions

90 northwards from southern central Europe without direct human assistance. A second set of four

91 invaders (here termed the Recent aliens) became established between 1990 and 2000 (Table 1, Fig.

92 S1), including the host-alternators *Andricus lucidus* (Stone & Sunnucks, 1992), *Andricus aries*

93 (Leach & Shirley, 1999, Walker 2001a) and *Andricus grossulariae* (Walker, 2001b), and one

94 species specific to *Q. cerris* - *Aphelonyx cerricola* (Crawley, 1997). All species in both sets were

95 first recorded in southern England (Table 1). Since 2000, five more invaders wholly dependent on

96 non-native oaks have reached Britain (Table 1). Because these most recent arrivals are in the

97 earliest stages of their establishment in Britain, and were too rare to allow sampling of associated

98 parasitoid communities, here we focus on the Early and Recent aliens with the following general

99   aims: (i) to update what is known of the U.K. distributions of species in both groups, (ii) to

100   estimate rates of geographic range expansion, and (iii) to describe the natural enemy communities

101   associated with each generation of all 8 species. This is the first comprehensive survey of the

102   Recent aliens, but builds on 30 years of previous work on the Early group, summarised below.

103

104   Surveys of the Early aliens in the 1990's found all four species to be widely distributed in

105   southern Britain. *Andricus kollari* was the most widespread species, extending into northern

106   Scotland, while *A. lignicolus* had reached southern Scotland, *A. quercuscalicis* had reached

107   Northumberland, and *A. corruptrix* was restricted to southern and central England (Schönrogge et

108   al., 1998; Walker et al. 2002). Studies of parasitoid recruitment from 1980-1990 focussed primarily

109   on the 'knopper' gallwasp, *A. quercuscalicis*, and on potential links between this species and native

110   gallwasps mediated by shared natural enemies (Hails et al., 1990; Hails & Crawley, 1991;

111   Schönrogge et al., 1996a; Schönrogge et al., 1998, 2000; Schönrogge & Crawley, 2000). Europe-

112   wide surveys found the parasitoid species attacking *A. quercuscalicis* in Britain to be only a subset

113   of those attacking it in its native range (Schönrogge *et al.,* 1995; Stone *et al.,* 1995), where galls of

114   both generations were attacked by parasitoids unknown in Britain. The species richness of

115   parasitoids associated with this invading host in Britain has increased over time (Schönrogge et al.,

116   1995, 1996b). Both temporal and spatial patterns could be explained by a lag in the ability of native

117   parasitoids to attack non-native gall phenotypes on an introduced oak host – a conclusion supported

118   by more general comparative analyses of host traits structuring oak gallwasp communities (Bailey

119   et al., 2009). An alternative (and compatible) explanation is that pursuit of the invading hosts by

120   parasitoids native to contiguous parts of continental Europe occurred only after a lag (Hayward &

121   Stone, 2005, 2006; Nicholls et al., 2010b). Support for parasitoid pursuit of invading hosts would be

122   provided by detection in UK samples of non-native parasitoids known to attack the invading gallers

123   in continental Europe. So far, only one alien parasitoid, the torymid *Megastigmus stigmatizans*, is

124 known to have reached Britain, both through host pursuit from the Balkans and introduction with *A.*

125 *kollari* from the Middle East (Nicholls *et al*. 2010b).

126

127   An additional finding of parasitoid surveys of Early aliens through the 1990's was that

128 parasitoids emerging from sexual generation galls of *A. quercuscalicis* on *Q. cerris* showed very

129 male-dominated sex ratios – particularly in the pteromalid parasitoids *Mesopolobus dubius*, *M.*

130 *fuscipes*, *M. tibialis* and *M. xanthocerus*. As a result, the alien hosts constituted a sink, but not a

131 source, for native parasitoid populations (Hails, 1989; Schönrogge et al., 1998, 2000). This

132 contrasts with more balanced sex ratios for the same parasitoid species attacking the same hosts in

133 their native continental European range (Stone *et al*. 1995).

134

135   Here we report changes in the British distributions of the Early aliens between the last

136 national surveys in 1992/3 (Walker et al., 2002) and 2004/5, and calculate their mean rates of

137 spread. We ask whether non-native parasitoids are now associated with these galls, as predicted by

138 the pursuit hypothesis. We report the ranges of the Recent aliens and detail their associated

139 parasitoid assemblages, and ask whether the sex ratios of *Mesopolobus* parasitoids attacking the

140 sexual generations of the Early aliens remain heavily male-biased. Finally, we ask whether

141 contrasts between native and invaded range parasitoid faunas associated with the Recent aliens

142 parallel those described in the past for the Early aliens, and particularly *A. quercuscalicis*.

143

Material and Methods

Gall surveys

146   The first national surveys in 1992 and 1993 sampled 256 locations (see site map,

147 supplementary figure S2) across the length and breadth of the UK selected on the basis of known

148 presence of *Q. robur/petraea* and/or *Q. cerris*, ranging from Berriedale (Caithness, UK grid

149 reference ND112225) in the north to Mawgawn (Cornwall, SW697204) in the south and west and

150 Westleton (Suffolk, TM430690) in the east (grid references for all survey sites are provided in

151   Table S1A). This provided the baseline for later surveys by Schönrogge et al. (1996a) and Walker et

152   al. (2002). In the autumn and spring of 2004 and 2005 we surveyed 118 sites throughout Britain

153   (Figs. 1, 2; location details are provided in Table S1B). While the two surveys provided good

154   overall coverage of mainland Britain, they did not visit the same set of sites; the 2004-2005 surveys

155   visited 10% of the sites visited in 1992-1993, and 35% of sites in 2004-2005 were within 10km of

156   sites sampled in 1992-1993. While this prevents any meaningful analysis of local population

157   dynamics, our density of sampling does allow detection of substantive range changes on a regional

158   scale. The earlier surveys were carried out in autumn when the galls of all the species in question

159   are larger and more conspicuous. During both surveys sites were searched for 1 hour for the galls of

160   invading species (see Fig. S1) by experienced fieldworkers.

161

162   **Estimating rates of spread**

163   The mean rate of spread for each species was calculated by dividing the straight-line

164   distance between the site of first record (Table 1) and the most distant UK record in 2004/5 by the

165   time interval between records in years. For two species – *A. aries* and *A. quercuscalicis* - more

166   extensive datasets (Tables S2, S3) allowed the fitting of more complex regression models of range

167   expansion. For each species, we tested the hypothesis of changing rates of spread during the

168   invasion process by fitting linear and quadratic terms. Dated records used in our analyses comprise

169   published records (Table 1), our own survey data, and unpublished records made available by the

170   British Plant Gall Society, regional wildlife trusts and Dr. R.R. Askew (Schönrogge, 1994).

171

172   **Gall collection and rearing**

173   Autumn asexual generation galls encountered at each survey site were collected up to a

174   standard upper sample size of 150/species, shown in previous analyses to be the assymptote in the

175   species sampling curve for associated parasitoids (Schönrogge et al. 2005, 2006a). The only

176   exception was the knopper galls of *A. quercuscalicis*, for which we collected samples of 150 galls

177 from a subset of 13 of the 118 survey sites spanning its current UK range (indicated by red symbols

178 in Figure 1b). This subsampling allows direct comparison with previous work on this species, and

179 was also necessary to limit to manageable levels the taxonomic load associated with identifying the

180 numerous occupants of these galls. All asexual generation galls were reared individually. When

181 sampling from native oaks, as in some previous work on oak-associated insect faunas (Bailey *et al*.

182 2009) we did not attempt to distinguish between pedunculate oak *Q. robur* and sessile oak *Q.*

183 *petraea*: widespread hybridisation between these species makes morphology-based discrimination

184 unreliable (Lepais *et al*. 2009).

185   The sexual generation galls of *A. corruptrix, A. kollari* and *A. lignicolus* on Turkey oak are

186 very small and cryptic (Fig.S1). Sampling them requires careful dissection of individual young buds

187 on *Q. cerris* shoots (defined as the past year's growth), and could not be attempted at all sites.

188 Instead, we sampled three sites used previously by Schönrogge & Crawley (2000), comprising

189 Silwood Park (SU942692) and Puttenham Common (SU494065) in southern England, and (for *A.*

190 *kollari* and *A. lignicolus* only) Dunrobin Castle (NC847007) in northern Scotland. We dissected all

191 buds on 1080 *Q. cerris* shoots at each southern site (6 shoots on each of 15 branches from 12 trees),

192 and at Dunrobin Castle we dissected buds on 540 shoots (6 shoots on each of 15 branches from the

193 six available trees). Overall, we reared 2428 bud galls from *Q. cerris*. Parasitoids attacking the

194 sexual generation catkin galls of *A. grossulariae* were sampled at Silwood Park (1911 galls) and

195 Puttenham Common (1093 galls). These samples were reared as individual catkins after removal of

196 any other catkin galls (only the sexual galls of *A. quercuscalicis* and *A. lucidus* in the U.K.; Fig.

197 S1). Though *A. aries* sexual generation galls have been identified (known to be bud galls on *Q.*

198 *cerris*, but not yet formally described; Walker 2001a), they were not detected in our sampling. All

199 sampled galls were reared in an outside insectary, and emerging adult insects were collected weekly

200 and identified. Subsamples of parasitoids were sent to Dr R. R. Askew (U.K.) to confirm

201 identifications. All emerging cynipid inquilines were identified to morphospecies using existing

202 keys (Pujade-Villar *et al*., 2003) by G.M., a recognised authority on this group. Recent DNA

barcoding work has revealed problems in the current morphological taxonomy of the Synergini

(Ács *et al*. 2010). We consider the impact of this for our surveys in the Discussion.

Results

The distributions of alien cynipid species in Britain

(a) Early aliens. The distribution of *Andricus kollari* (Fig. 1a) shows no significant change since

1992/3. It remains widespread throughout Britain but absent from large areas of northwestern

Scotland. *Andricus lignicolus* (Fig. 1c) has expanded northwards into northeastern Scotland

(Dunrobin Castle, NC848008), but is also absent from large areas of the northwest. *Andricus*

quercuscalicis (Fig. 1b) has expanded into north-central Scotland, reaching just south of Glenshee

in Perthshire (NO304742). *Andricus corruptrix* (Fig. 1d) has now reached Ripon in North Yorkshire

(SE355678), but continues to lag behind *A. lignicolus*, despite being first recorded in the same year

and U.K. county (Table 1).

(b) Recent aliens. These species remain largely restricted to southern and southeastern England

(Fig. 2 a-d). From its first record in Richmond Park, London (TQ200731), in 14 years *Andricus*

lucidus (Fig. 2a) has spread 61km as far as Scotney Castle in Kent (TQ692359, Table 1). *Aphelonyx*

cerricola (Fig. 2c) is the least mobile species in this group, and has spread only 14km from its first

record at Maidenhead (SU852807) in 1997 to Windsor (SU964725) in 2006 (Table 1). In contrast,

A. aries (Fig. 2b) and *A. grossulariae* (Fig. 2d) have spread much further. Between 1997 and 2007

Andricus aries spread 214km from southeastern England (Maidenhead, Berkshire, SU8582) to

northwestern England (Malpas, Cheshire, SJ471455) (Table S1), while between 2000 and 2007 *A.*

grossulariae spread 140km from southeastern England (Ascot, Berkshire SU947687) westwards

into Hampshire (Winfrith, SY810873), and 80km eastwards to Edney Common, Essex by 2008

(Table S1).

Rates of spread of invading cynipids

230   (a) Rates estimated using start and end points of range expansion. Among the Early aliens, the first

231   species to arrive - *A. kollari* – took 52 years to disperse *circa* 850km from the Ex Valley, Devon

232   (1834) to near the limits of its current Scottish distribution (1882), with a mean rate of linear spread

233   of 16.4 km/year. *Andricus lignicolus* shows the highest rate of any invading gallwasp at

234   24.4km/year while *A. quercuscalicis* and *A. corruptrix* have somewhat lower rates at 10.6 and 9.3

235   km/year respectively. The more extensive data for *Andricus quercuscalicis* (Table S3) allow us to

236   compare rates of expansion across Europe with those across Britain. From its first record outside its

237   native range, at Gera in Germany (1631), *Andricus quercuscalicis* took 372 years to disperse

238   1241km to reach Balloch (NS 388835) near Glasgow in 2003, with an average linear rate of spread

239   of only 3.3 km/year. The rate of range expansion measured from its first British record at Salcey

240   Wood in Northamptonshire (SP793514) in 1961 is 10.6 km/year, more than three times the rate

241   measured over the entire invaded range.

242   Among the Recent aliens, rates of spread are high in two species (19.9km/year in *A.*

243   *grossulariae* and 21.4 km/year in *A. aries*), and much lower in two others (4.4km/year in *A. lucidus*

244   and 1.4 km/year *Aphelonyx cerricola*).

245

246   (b) Regression analyses for *A. aries* and *A. quercuscalicis*. Data for *A. aries* (Table S2) support a

247   constant rate of spread of 19.8 ($\pm$2.3 standard error) km/year (Fig. 3a), with no support for a model

248   that allows the rate to increase or decrease over time (linear model $F_{1,9} = 49.44$, $p < 0.001$, $R^2_{adj} =$

249   84.3; sequential ANOVA with quadratic model $F_{1,9} = 0.77$, $p \gg 0.05$). For *Andricus quercuscalicis*,

250   regression analysis across Europe also supported a constant rate of spread of 3.4 ($\pm$0.5) km/year

251   (Fig 3b), although a quadratic model incorporating an exponentially increasing rate of spread was

252   nearly significant (linear model $F_{1,8} = 57.79$, $p < 0.001$, $R^2_{adj} = 87.7$; sequential ANOVA with

253   quadratic model $F_{1,8} = 4.99$, $p = 0.067$), perhaps due to the leverage of the earliest record.

254   Regression analysis within the UK estimated a constant rate of spread of 11.4 ($\pm$0.7) km/year (Table

255   S3, Fig 3c; linear model $F_{1,4} = 29.26$, $p = 0.012$), again with no significant quadratic term (quadratic

256 model $F_{1,4} = 0.61$, p = 0.517). In both species, estimates derived from regression analyses agree well

257 with distance calculations based on point of the first record to the furthest point along the invasion

258 front, suggesting that the simpler approach probably provides a reasonable estimate of rates in the

259 remaining alien gallwasp species.

260

261 ***Parasitoid and inquiline species associated with alien gallwasps in Britain***

262 (i) *Sexual generation parasitoid assemblages on Turkey oak*. Parasitoid and inquiline assemblages

263 for sexual generation galls are summarised in Table 2. Among the Early alien species, our surveys

264 extended previously known assemblages only for *A. quercuscalicis*, which has recruited 3 new

265 parasitoids - *Cecidostiba fungosa* and *Mesopolobus sericeus* (Pteromalidae)*,* and *Ormocerus*

266 *vernalis* (Eulophidae). Detailed analyses of the sex ratios (number of males/males+females) of

267 *Mesopolobus* species reared from sexual *A. quercuscalicis* galls remain heavily male biased. In

268 2005 and 2006 1284 and 523 galls respectively were reared from Silwood Park and 495 and 598

269 galls from Puttenham Common. Sex ratios of the four *Mesopolobus* species were found to be: *M.*

270 *dubius* (average±SE, no. of parasitoids reared: 1±0, 14), *M. fuscipes* (0.98±0.02, 275), *M. tibialis*

271 (0.87±0.05, 308) and *M. xanthocerus* (0.99±0.01, 183).

272   Among the Recent aliens, all of the known sexual generations have recruited parasitoids

273 (Table 2). Despite its recent arrival, the highest numbers of parasitoid and inquiline species in any

274 alien sexual generation gall (15), whether Early or Recent, were reared from the Recent alien *A.*

275 *grossulariae* (Table 2). One interesting new rearing record was for an endoparasitoid, *Sycophila*

276 *biguttata* (Eurytomidae), reared from sexual generation galls of *A. lucidus*. This parasitoid is rare in

277 sexual generation oak galls, and we reared two females from 55 galls collected at Silwood Park and

278 5 from 12 galls collected at Puttenham Common. Only one inquiline morpho-species – *Synergus*

279 *gallaepomiformis* – was reared from any of the sampled sexual galls (*A. grossulariae*). All of the

280 sexual generation parasitoid and inquiline species we detected have been previously recorded in

281 Britain.

282

283   (ii) *Asexual generation parasitoid assemblages on sessile and pedunculate oak.* Among the Early

284   aliens, parasitoid species richness associated with galls of this generation ranged from 6 species in

285   *A. lignicolus* to 18 in *A. kollari* (Table 3). The only new assemblage members in asexual generation

286   galls for Early aliens were the inquiline *Synergus pallipes* from *A. quercuscalicis*, and a single

287   specimen of the inquiline *Ceroptres clavicornis* from *A. kollari*. The Recent aliens produced many

288   new host records for known British parasitoids and inquilines (Table 4), including 12 for *Aphelonyx*

289   *cerricola*, 10 for *A. aries* and *A. grossulariae*, and 9 for *A. lucidus*. However, no new (non-native)

290   parasitoid or inquiline species were detected. Inquilines make a much greater contribution to

291   community species richness in this generation than in the sexual generations.

292

293   **Discussion**

294   Although biological invasions have long been seen as windows on the process of

295   community assembly (Sax et al., 2007), the invasion of U.K. by oak gallwasps is one of very few

296   long-term studies of multiple parallel invasions by related species (Schönrogge et al., 1998;

297   Schönrogge & Crawley, 2000; Hayward & Stone, 2005). The shared dependence of the study

298   species on distributions of just two host oak species, and hence dependence on the same set of

299   habitat patches, removes one of the major difficulties in comparing range expansion processes

300   across species, allowing us to draw conclusions across a herbivore guild.

301

302   *Patterns of range expansion*

303   All but one of the early invaders (*A. kollari*) have continued to expand their ranges

304   northwards across Britain. The 2005 surveys showed this species to be widespread through all but

305   the furthest northwestern parts of Scotland. *Andricus lignicolus* is now almost as widespread as *A.*

306   *kollari* in Scotland (where it was first recorded in 1996 by Entwistle (1996)), with similar northern

307   limits and absence from the northwest, including the Outer Hebrides. We suggest that this rarity

308   stems from the fact that all oaks, and particularly *Q. cerris*, are relatively rare and very patchily

309   distributed in this part of Scotland (Walker et al., 2002), predicting similar limits to range expansion

310   for all alien gallwasps. *Andricus quercuscalicis* continues to expand through Scotland, where it was

311   first reported in Edinburgh in 1998 (G. Stone, unpublished; see also Muscot 2001) and in south-

312   western Scotland in 2001 (Hancock 2001). As in England its asexual generation 'knopper' galls can

313   be extremely abundant on *Q. robur* with heavy acorn crops, and in addition to our surveys it was

314   recorded in 2002-3 from sites across Lanarkshire, Renfrewshire, and Perthshire (Table S4).

315   *Andricus corruptrix* continues to lag behind the other Early alien species, with little range

316   expansion over the last 10 years: in 1996 it was recorded as far west as Somerset (Walker et al.,

317   2002) and as far north as Yorkshire and Lincolnshire (Shirley, 1998; Walker et al., 2002), while by

318   2004-5 its western limit had extended to Devon and the northern limit to North Yorkshire. This

319   slow rate of spread may be due in part to under-recording, since both generations of *Andricus*

320   *corruptrix* are relatively cryptic (Fig. S1).

321

322   Our surveys establish baseline distributions allowing tracking of ongoing range expansion

323   by the Recent aliens *A. aries, A. lucidus, A. grossulariae,* and *Aphelonyx cerricola.* All eight alien

324   species show parallel invasion trajectories from south-eastern Britain to the north and west, a

325   continuation of the invasion processes that (with the exception of *A. kollari*) brought them to the

326   Channel coast from central Europe (Stone & Sunnucks, 1993; Csóka et al., 1998; Stone et al., 2001;

327   Hayward & Stone, 2005; Stone et al., 2007). While the species spread at different rates, there is no

328   indication of any geographic or ecological barrier other than rarity of *Q. cerris* that would prevent

329   continued range expansion across Britain (Walker et al. 2002). *Aphelonyx cerricola* is the only

330   species in this set of 8 that is wholly dependent on *Q. cerris*, and also the only species to have a

331   single generation each year in its lifecycle. Notably, it has the lowest rate of spread and has

332   expanded its range very little since arriving in the UK (Table 2). However, as shown by *A. lucidus,*

333   bivoltine and host-alternating species can also have low rates of spread. More striking perhaps is the

334   5.5-fold variation in expansion rates among host-alternating species with similar dependence on the

335   same oaks. This variation may reflect sampling error (for example, in estimates of arrival dates at

336   sampled locations), or it may reflect genuine variation in species range expansion processes.

337

338   Dispersal patterns during invasions are particularly important for understanding the

339   dynamics of biogeographical patterns, particularly those expected in response to climate change

340   (Kinlan & Hastings, 2005). Phylogeographic studies of *A. quercuscalicis* (Stone & Sunnucks,

341   1993), *A. kollari* (Hayward & Stone. 2005; Stone *et al*., 2007), *A. corruptrix* and *A. lignicolus*

342   (Csóka et al., 1998) in their European invaded range all support 'stepping stone' dispersal between

343   ecological islands of *Q. cerris* in a more uniform 'sea' of native Q*. robur/petraea*. The documented

344   higher density of *Q. cerris* in Britain and Holland relative to eastern France and northern Germany

345   (Jalas & Suominen, 1976) probably also explains a degree of increase in mean rate of spread for *A.*

346   *quercuscalicis*. The only alien gallwasp known to receive human assistance during dispersal within

347   Britain is *A. lignicolus*, which was introduced to central Scotland within 15 years of its arrival via

348   transport of galled oaks by horticultural suppliers (Walker et al., 2002). Though not documented for

349   the other species, this mechanism may well also have contributed to their dispersal. However, over

350   a shorter time- and geographical scale, the linear rate of spread shown by *A. aries* suggests rapid

351   and uniform diffusion dispersal (Okubo & Levin, 2002), without major jumps in distribution due to

352   human assistance. We note that the most recently invading gallwasps include *Plagiotrochus* species

353   associated with *Quercus ilex* for which the first records are in the southwest of Britain rather than

354   the southeast. It remains to be seen how the contrasting host association and sites of first records for

355   *Plagiotrochus* species influences their rate of spread through the UK.

356

357   ***Parasitoid and inquiline assemblages***

358   The parasitoid and inquiline assemblages associated with both generations of the Early

359   alien gallwasps have remained largely unchanged since the last survey in 1994/5 (Schönrogge et al.,

360   1996b; Schönrogge et al., 2000), with only 3 new parasitoid records for *A. quercuscalicis* sexual

361   galls (*C. fungosa, M. sericeus* and *O. vernalis*), one new inquiline record for *A. quercuscalicis*

362   asexual galls (*S. pallipes*) and one new inquiline record for *A. kollari* asexual galls (*C. clavicornis*).

363   Earlier studies that considered parasitoid emergence from both native and alien hosts

364   showed that galls of alien species on *Q. cerris* had become by far the most important hosts to

365   parasitoids such as *M. dubius*, *M. fuscipes*, *M. tibialis* and *M. xanthocerus*, but also that parasitoid

366   emergence from the most abundant resource, the sexual galls of *A. quercuscalicis*, was virtually

367   male-only at the population level in 13 out of 16 samples (Schönrogge & Crawley 2000;

368   Schönrogge et al. 2000). One might expect the parasitoid species to evolve such that they can

369   develop female offspring on the smaller *A. quercuscalicis* hosts, but sex ratios observed here give

370   no indication that this is happening.

371   In contrast, the parasitoid assemblages of the Recent aliens are developing rapidly. Of

372   particular interest are 15 species (14 species of parasitoids and one inquiline cynipid) reared from

373   the sexual generation of *A. grossulariae* galls on *Q. cerris*. This compares to 25 parasitoid species

374   known to attack these galls on the continent (Chust et al., 2007; Melika et al., 2002). All 14

375   parasitoid species recorded from sexual *A. grossulariae* are on the British list and have been reared

376   from other cynipid galls in the past (Askew 1961, Noyes 2003), suggesting that these parasitoids are

377   recruited natives. Three of those species, *Sycophila flavicollis*, *Mesopolobus sericeus* and *Torymus*

378   *flavipes*, are interesting because they are not known to attack the same host galls in their native

379   continental range. Of the 12 species known to attack sexual *A. grossulariae* in continental Europe

380   that are not yet recorded from this gall in Britain, 8 are known in Britain (*Eupelmus annulatus*,

381   *Eurytoma pistaciae*, *Ormyrus pomaceus*, *Ormocerus latus*, *Hobbya stenonota*, *Aulogymnus*

382   *gallarum*, *A. trilineatus* and *Aprostocetus aethiops*), and so are likely to be recruited in future if

383   patterns in *A. grossulariae* mimic those in other invading oak cynipid communities in the UK

384   (Schönrogge et al. 1995; 1996a,b; 1998). The remaining 4 species (*Aprostocetus cerricola*, *A.*

385   *domenichinii*, *Aulogymnus obscuripes* and *Mesopolobus lichtensteini*) are unknown in Britain, and

386   their detection in *A grossulariae* galls in the future would suggest parasitoid pursuit of this invader

387   from the continent (Melika et al., 2002; Noyes 2003).

388   Three of the native parasitoid species that attack *A. grossulariae* sexual galls (*Mesopolobus*

389   *fuscipes, Mesopolobus tibialis* and *Mesopolobus xanthocerus*) are generally associated primarily

390   with hosts on Turkey oak, including the sexual generation galls of the Early alien species, rather

391   than native gallwasps on native oaks (Schönrogge et al., 2000). Invading and introduced gallwasp

392   hosts are now the dominant host resources for these parasitoids in Britain (Schönrogge et al., 2000).

393   The remaining parasitoids attacking *A. grossulariae* sexual generation galls in Britain are shared

394   with native gallwasp hosts on *Q. petraea* and *Q. robur*, linking the previously almost entirely

395   separate parasitoid communities on the two tree species in spring and providing the potential for

396   indirect competitive interactions between them (Schönrogge & Crawley, 2000; Kenis et al., 2009).

397

398   Both generations of all the Recent alien gallwasp species (with the exception of the

399   undetected sexual generation of *A. aries*) yielded parasitoid records, even if the sexual generation

400   galls of *A. lucidus* yielded only one parasitoid species, *S. biguttata*. This contrasts with the early

401   invasion history of the best-studied species of the eight, *A. quercuscalicis*, whose asexual generation

402   knopper galls were intensively reared since the 1970's, and remained virtually free of parasitoids or

403   inquilines through the 1980's (Collins et al., 1983; Hails et al., 1990). The assemblages associated

404   with knopper galls increased in abundance and species richness rapidly through the early 1990's

405   (Schönrogge et al., 1996a, b). At that time, the asexual 'knopper' galls of *A. quercuscalicis* were the

406   only large, structurally complex galls to be induced on the acorns of *Q. robur*, representing a novel

407   resource that we suggest was initially undetected or immune to attack by native parasitoids. The

408   structurally less complex sexual galls yielded parasitoids when first reared in the 1980's (Hails &

409   Crawley, 1991, 1992; Stone et al., 1995), despite their development on a non-native oak, *Q. cerris*.

410   However, in contrast to the asexual generation galls of *A. quercuscalicis*, the sexual generation galls

411   on catkins of *Q. cerris* are structurally very similar to those induced in buds by *A. kollari,* and these

412   had been available for parasitoid attack since the mid-nineteenth century (Walker et al., 2002). We

413   suggest that the sexual generation galls recruited enemies more rapidly because they were a more

414   familiar resource. This hypothesis is consistent with the conclusions of a large, comparative

415   analysis of the determinants of oak cynipid parasitoid communities (Bailey et al., 2009), which

416   found galls of similar structure on the same oaks to support significantly similar parasitoid

417   assemblages, while galls with very different external morphologies support significantly different

418   assemblages. The study also found any escape from enemies over evolutionary time associated with

419   evolution of novel gall phenotypes to be transient. Most gall phenotype combinations exist, and all

420   are attacked by parasitoids; while evolution of a new gall phenotype for a particular gallwasp

421   lineage may result in loss of some long-associated parasitoids, such phenotypes soon recruit

422   parasitoids already attacking phenotypically similar galls in the community (Bailey et al., 2009).

423   We suggest that once parasitoids began to exploit *A. quercuscalicis* asexual galls in the "acorn on

424   *Q. robur*" niche, they were in place to be recruited more rapidly by subsequent alien gallwasps

425   appearing on acorns of *Q. robur* (asexual generation *A. grossulariae* and *A. lucidus*). Similar

426   patterns of rapid recruitment of generalist natural enemies to invading hosts have been observed in

427   other systems, including leaf-mining moths (Godfray et al., 1995; Grobler & Lewis, 2008).

428

429   Our data for inquiline cynipids show that only one species is associated with any invading

430   sexual generation gall (*S. gallaepomiformis*), while 11 morphospecies are recorded from the asexual

431   generation galls. This contrast between gallwasp generations parallels that seen in all previous

432   surveys of these species (e.g. Hails, 1989; Stone et al., 1995, Schönrogge et al., 1995, 1996a, b,

433   1998, 2000), and probably reflects the contrast in morphological complexity and resource

434   availability to inquilines in the sexual galls (usually small, rapidly developing) and asexual galls

435   (larger, more complex, prolonged development) (Stone & Cook, 1998; Bailey *et al*., 2009). It is

436   noteworthy that the inquiline was recorded from *A. grossulariae* sexual galls, which (like the sexual

437   generation of *A. lucidus*) are far more structurally complex and long-lived than the sexual

438   generation galls of the Early aliens. The true diversity of inquiline cynipids associated with

439   invading cynipids, and identification of any host specificities among them, must await DNA-based

440   analysis, because while some morphospecies apparently represent discrete biological entities (and

441   so are 'good' biological species), others do not. Among the inquiline morphospecies identified in

442   our surveys, sequence based analysis (Ács *et al.*, 2010) shows some morphospecies to represent

443   morphological diversity within a single lineage (*S. gallaepomiformis, Synergus pallicornis,*

444   *Synergus pallidipennis* and *S. pallipes*), while one of the morphospecies (*Synergus umbraculus*)

445   incorporates several morphologically cryptic but phylogenetically distinct, non-monophyletic

446   lineages.

447

448   ***Community assembly in invading gallwasps***

449   The eight alien gallwasp species studied here are a subset of at least 9 species representing

450   17 gall types that have extended their distributions into contiguous areas of north-western Europe

451   from native ranges south of the Alps and Carpathians (Csóka et al., 2005; Stone et al., 2002). While

452   in the past biogeographic areas were regarded as relatively static entities characterised by

453   environmental parameters and the species living within them, there is a growing realisation that

454   biological assemblages can be much more dynamic (Hengeveld, 1988; Kinlan & Hastings, 2005).

455   Cynipid gallwasps provide a model for the increased movement of species, whether due to direct

456   human transport or by unassisted range expansion towards higher latitudes and altitudes in response

457   to climate change (Parmesan and Yohe, 2003). It has been suggested that climate change could

458   cause concordant range shifts by the multiple species defining biogeographic provinces, such that

459   entire existing assemblages move together (Thomas et al., 2004). An alternative view is that species

460   will move according to species-specific traits, determined in part by interactions with other species

461   (Jackson & Williams, 2004). The establishment of alien cynipids in Britain shows that once *Q.*

462   *cerris* was planted north of the Alps these species were able to extend their ranges north and west to

463   the continental boundaries, clearly demonstrating that their native distribution was the result of

464 biotic limitation rather than physiological tolerance. To date, all of the parasitoid species they have

465 recruited in Britain (with the exception of *M. stigmatizans* co-introduced with *A. kollari)* are natives

466 previously recorded from other gallwasp hosts in Britain. Though gallwasp invasions have triggered

467 pursuit by parasitoids (Hayward *et al.* 2005; Nicholls et al., 2010b) across continental Europe, there

468 is no evidence yet of parasitoid pursuit into Britain. None of the parasitoid species attacking the

469 invaders in continental Europe but previously unrecorded in Britain have been recorded since their

470 hosts arrived (Askew, 1961; Bouček & Graham, 1978; Schönrogge et al., 1995; Stone et al., 1995;

471 Melika et al., 2002). That these parasitoid species have not dispersed in parallel with their invading

472 hosts suggests either that they do not share the same broad environmental tolerances as the

473 gallwasps, have lower intrinsic dispersal or population growth rates, have higher population

474 extinction rates, or depend on the presence of other species (e.g. as alternate hosts) that also have

475 yet to expand their ranges. On a timescale of decades, these communities do not move as units, but

476 reassemble in a way that reflects local species pools and assembly rules defined by host niches

477 (Schönrogge et al., 1995; Bailey et al. 2009). As a result, British parasitoid and inquiline

478 assemblages associated with the invaders will only converge on those in their native range if

479 continental parasitoids currently absent from Britain pursue their hosts over longer timescales.

480 Phylogeographic analyses of continental European parasitoid populations show that host pursuit

481 does occur in this system over a timescale of centuries (Hayward & Stone 2005) and millennia

482 (Nicholls *et al.* 2010a,b).

483

488

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490
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Table and Figure headings

Table 1 Documented first records and locations for alien gallwasps in Britain.

Table 2 Parasitoid and inquiline species recorded from the sexual generation galls of alien gallwasps in Britain. Sources of literature records are indicated by numbers in brackets in table cells as follows: 1. Mayr (1903); 2. Schönrogge *et al*. (2000); 3. Hails and Crawley (1991); 4. Askew (1961); 5. Mayr (1905); 6. Askew (1966); 7. Marsden-Jones (1953); 8. Eady (1952); 9. Schönrogge *et al*. (1995); 10. Schönrogge *et al*. (1996); 11. Askew and Neill (1993); 12. Wurzell (2000); 13. Jennings (2001). Records without a reference are new host records for the UK.

Table 3 Parasitoid and inquiline species recorded from the asexual generation galls of Early alien gallwasps, reaching Britain before 1992. Sources of literature records are indicated by numbers in brackets in table cells – for references see legend to Table 2. Records without a reference are new host records for the UK.

Table 4 Parasitoid and inquiline species recorded from the asexual generation galls of Recent alien gallwasps, reaching Britain after 1992. Sources of literature records are indicated by numbers in brackets in table cells – for references see legend to Table 2. Records without a reference are new host records for the UK.

Figure 1 The distributions of Early alien gallwasps in the 2004-05. Filled circles indicate presence, open circles absence. (a) *Andricus kollari*, (b) *A. quercuscalicis* (the 13 collection sites for rearings are indicated by a red symbol), (c) *A. lignicolus*, (d) *A. corruptrix*.

Figure 2 The distributions of Recent alien gallwasps in the 2004-05. Filled circles indicate presence, open circles absence. (a) *A. lucidus,* (b) *Andricus aries,* (c) *Aphelonyx cerricola*, (d) *Andricus grossulariae*.

Figure 3. a) The linear rate of spread of *Andricus aries* in Britain since its first record in 1996. b) The historical rate of spread of *Andricus quercuscalicis* across Europe since the first record outside the native range in Gera, Germany, in 1631. c) Spread of *A. quercuscalicis* after its arrival in Britain in 1961. Analytical results are given in the main text. Dashed lines in the figures show 95% confidence intervals of fitted models.

744 **Tables and Figures**

745

746 **Table 1:**

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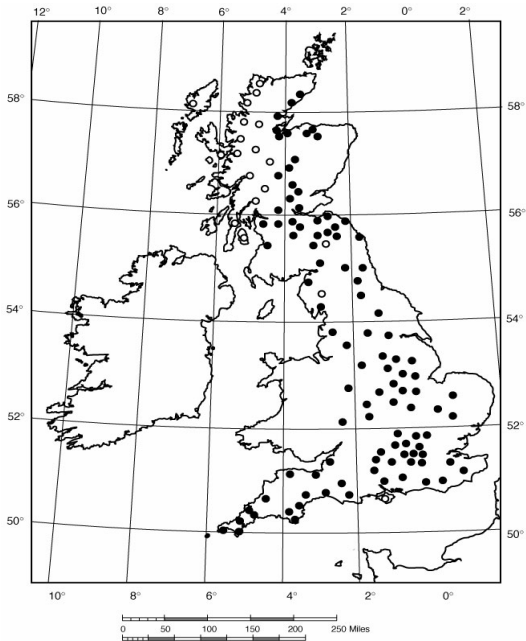| Early vs. Recent aliens	Species	Generations and host-trees	Year of 1st record	Location	Reference
Early	*Andricus kollari*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1834	Exe Valley, Devon (approx. SS91)	Smith (1854)
Early	*Andricus quercuscalicis*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1961	Salcey Wood, Northamptonshire (SP793514)	Claridge (1962)
Early	*Andricus lignicolus*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1974	Wiggonholt Common, West Sussex (TQ060163)	Hutchinson (1974, but also see Walker et al. 2002)
Early	*Andricus corruptrix*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1974	Wiggonholt Common, West Sussex (TQ060163)	Hutchinson (1974, but also see Walker et al. 2002)
Recent	*Andricus lucidus*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1992	Richmond, London (TQ2072)	Stone and Sunnucks (1992)
Recent	*Andricus aries*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	1997	Maidenhead, Berkshire (SU8582)	Walker (2001a)
Recent	*Aphelonyx cerricola*	One generation on *Q. cerris*	1997	Maidenhead, Berkshire (SU8582)	Crawley (1997)
Recent	*Andricus grossulariae*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	2000	Ascot, Berkshire (SU947687)	Walker (2001b)
Recent	*Plagiotrochus quercusilicis*	One generation on *Q. ilex* (a second generation is suspected to exist)	2004	Bodelva, Cornwall (SX0454)	Hancy and Hancy (2004)
Recent	*Neuroterus saliens*	Spring: *Q. cerris* Autumn: *Q. cerris*	2006	Hackney, London (TQ3487)	Redfern (2006)
Recent	*Plagiotrochus australis*	Two generations on *Q. ilex*	2007	Glamorgan, Wales (SN8813)	Robbins (2007)
Recent	*Plagiotrochus coriaceus*	One generation on *Q. ilex*	2007	Glamorgan, Wales (SN8813)	Robbins (2007)
Recent	*Andricus gemmeus*	Spring: *Q. cerris* Autumn: *Q.robur/petraea*	2008	Colchester, Essex (TM0023)	Bowdrey (2009)

748

749

750 **Table 2**

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Family	Parasitoid species	*Andricus kollari*	*Andricus quercuscalicis*	*Andricus lignicolus*	*Andricus corruptrix*	*Andricus lucidus*	*Andricus grossulariae*
Eulophidae	*Aprostocetus aethiops*	-	√ (3)	-	-	-	-
	Ormocerus vernalis	-	√	-	-	-	-
Eupelmidae	*Eupelmus urozonus*	-	-	-	-	-	√
Eurytomidae	*Eurytoma brunniventris*	-	-	-	-	-	√
	Sycophila biguttata	-	-	-	-	√	√
	S. flavicollis	-	-	-	-	-	√
	S. variegata	-	-	-	-	-	√
Pteromalidae	*Cecidostiba fungosa*	-	√	-	-	-	√
	Mesopolobus amaenus	-	-	-	-	-	√
	M. dubius	-	√ (3)	√ (2)	√ (2)	-	-
	M. fuscipes	√ (1)	√ (4)	√ (2)	√ (2)	-	√
	M. sericeus	-	√	-	-	-	√
	M. tibialis	√ (2)	√ (4)	√ (2)	-	-	√
	M. xanthocerus	√ (2)	√ (4)	√ (2)	√ (2)	-	√
Torymidae	*Megastigmus dorsalis*	-	-	-	-	-	√
	Torymus flavipes	-	-	-	-	-	√
Ormyridae	*Ormyrus nitidulus*	-	-	-	-	-	√
	Cynipid inquilines						
	Synergus gallaepomiformis	-	-	-	-	-	√
Species richness		3	8	4	3	1	15

752

753 **Table 3**
754

| Family	Parasitoid species	*Andricus kollari*	*Andricus quercuscalicis*	*Andricus lignicolus*	*Andricus corruptrix*
Eulophidae	*Aulogymnus trilineatus*	√	-	-	-
Eupelmidae	*Eupelmus annulatus*	√	-	-	-
	E. urozonus	√ (4)	√ (9)	√ (11)	√ (2)
	E. vesicularis	-	√	-	-
Eurytomidae	*Sycophila biguttata*	√ (5)	√ (9)	-	√ (2)
	S. flavicolis	√ (4)	-	-	-
	S. variegata	√	-	-	√
	Eurytoma brunniventris	√ (4)	√ (9)	√	√ (2)
Ormyridae	*Ormyrus nitidulus*	-	√ (9)	-	-
	O. pomaceus	-	-	-	√ (2)
Pteromalidae	*Caenacis lauta*	√ (4)	-	-	-
	Cecidostiba fungosa	√ (2)	√ (9)	-	√ (2)
	C.semifascia	-	√ (10)	-	-
	Hobbya stenonata	√ (4)	-	-	-
	Mesopolobus amaenus	√ (4)	√ (10)	√ (12)	√ (2)
	M. fasciiventris	√	-	-	√ (2)
	M.sericeus	√	√ (9)	√ (11)	√ (2)
	M. tibialis	√ (2)	√ (2)	-	-
Torymidae	*Megastigmus dorsalis*	√ (6)	√ (9)	√ (11)	√
	M.stigmatizans	√ (6)	√ (9)	-	-
	Torymus auratus	√ (7)	√ (9)	√ (11)	-
	T. flavipes	-	-	-	√ (2)
	T. geranii	√ (4)	√ (3)	-	-
	Cynipid inquilines				
	Ceroptres clavicornis	√	-	-	-
	Synergus gallaepomiformis	√ (2)	√ (2)	√ (2)	√ (2)
	S. pallicornis	-	√ (3)	-	-
	S.pallidipennis	√ (8)	-	-	-
	S. pallipes	√ (2)	√	-	-
	S. radiatus	-	√ (2)	-	-
	S. reinhardi	√ (2)	-	√ (2)	√ (2)
	S. umbraculus	√ (2)	√ (9)	√ (11)	-
Species richness		24	19	9	12

755

756 **Table 4**

757

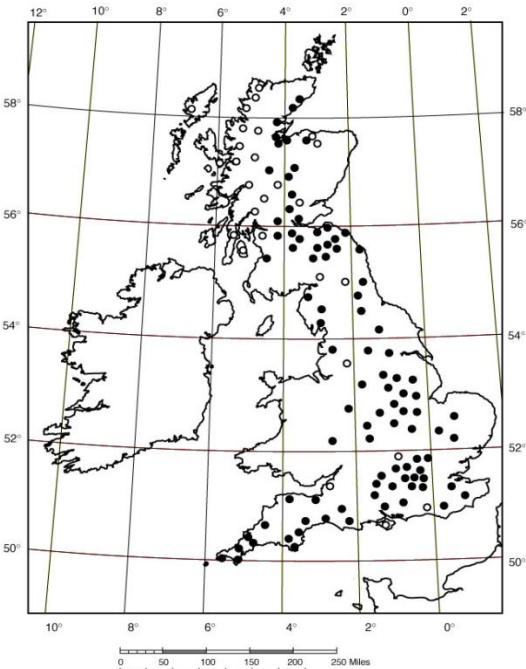| Family	Parasitoid species	*Andricus grossulariae*	*Andricus aries*	*Andricus lucidus*	*Aphelonyx cerricola*
Eurytomidae	*Sycophila biguttata*	√	√(13)	√	√
	S. flavicollis	-	√(13)	-	-
	S. variegata		√	-	-
	Eurytoma brunniventris	√	-	√	√
Torymidae	*Megastigmus dorsalis*	√	√ (12)	-	√
	Torymus auratus	-	-	√	√
	T. flavipes	-	√	-	-
Ormyridae	*Ormyrus nitidulus*	√	√	-	√
	O. pomaceus		-	-	√
Pteromalidae	*Cecidostiba fungosa*	√	√	√	√
	C. semifascia	-	-	-	√
	Mesopolobus sericeus	√	-	√	√
	M. xanthocerus	√	-	√	-
Eupelmidae	*Eupelmus urozonus*	√	-	√	-
	Cynipid inquilines				
	Ceroptres clavicornis	-	√	√	-
	Synergus gallaepomiformis	√	√(12)	-	√
	S. pallidipennis	-	√	-	-
	S. radiatus/pallipes	-	√	-	-
	S. reinhardi	-	√ (13)	-	-
	S. tibialis	-	√	-	-
	S. umbraculus	√	-	√	-
	S. incrassatus	-	-	-	√
	S. pallicornis	-	√	-	-
	S. rotundiventris	-	√	-	-
	S. variabilis	-	-	-	√
Species richness		10	15	9	12

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759

760   **Figure 1**

761   a) *Andricus kollari*   b) *Andricus quercuscalicis*

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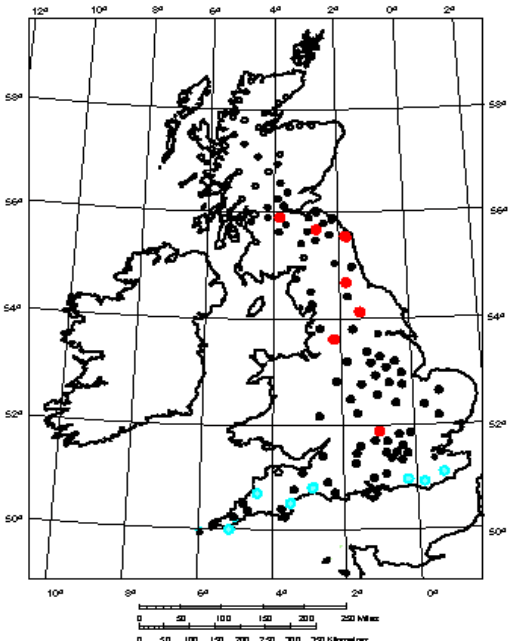
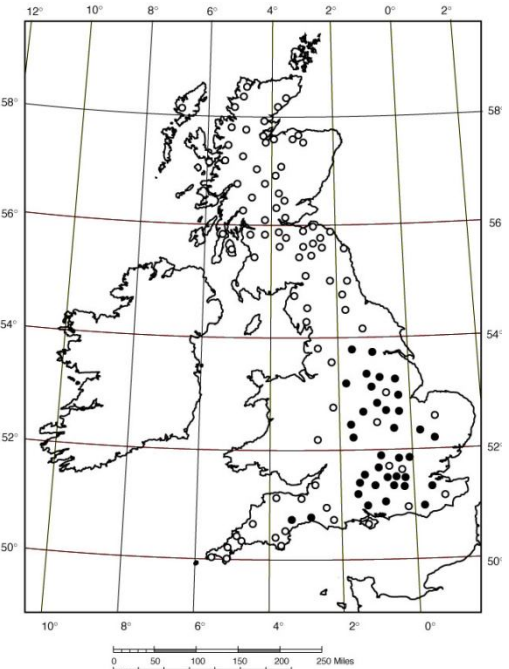763   *c) Andricus lignicolus*   *d) Andricus corruptrix*

764

765   **Figure 2**

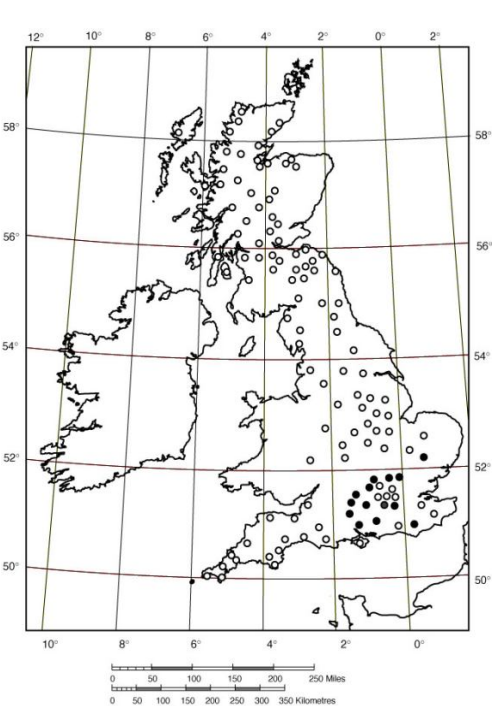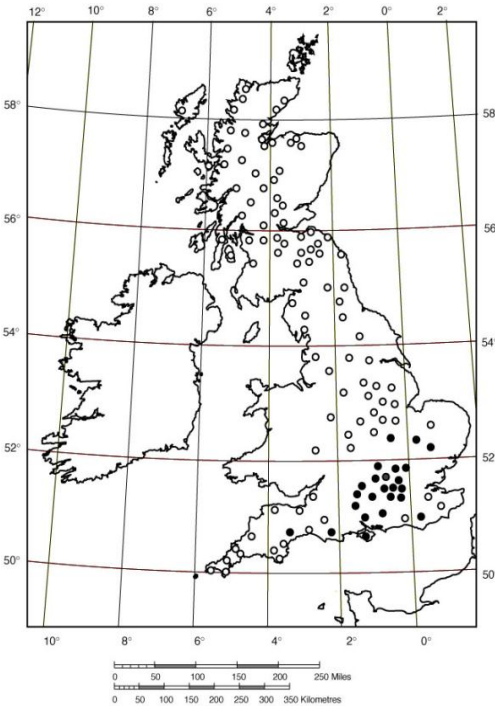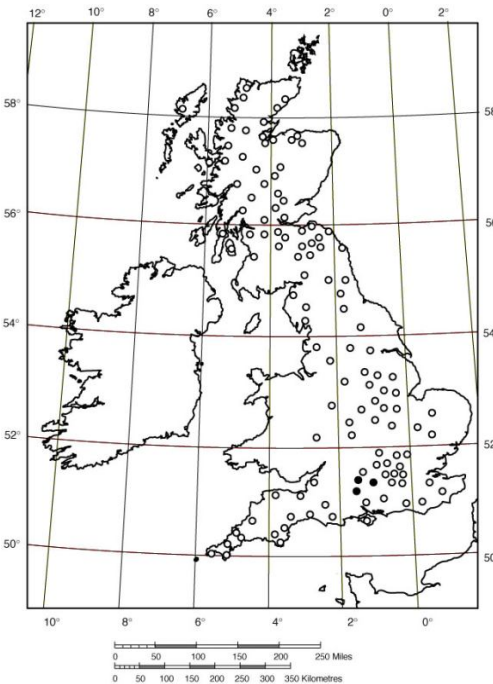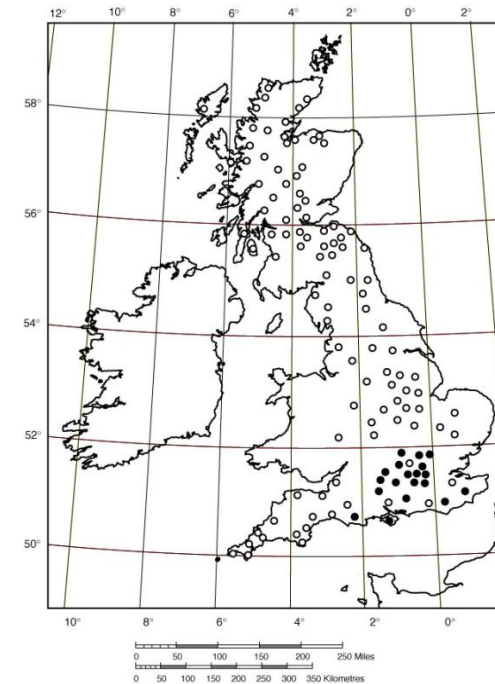766   a) *Andricus lucidus*   b) *Andricus aries*
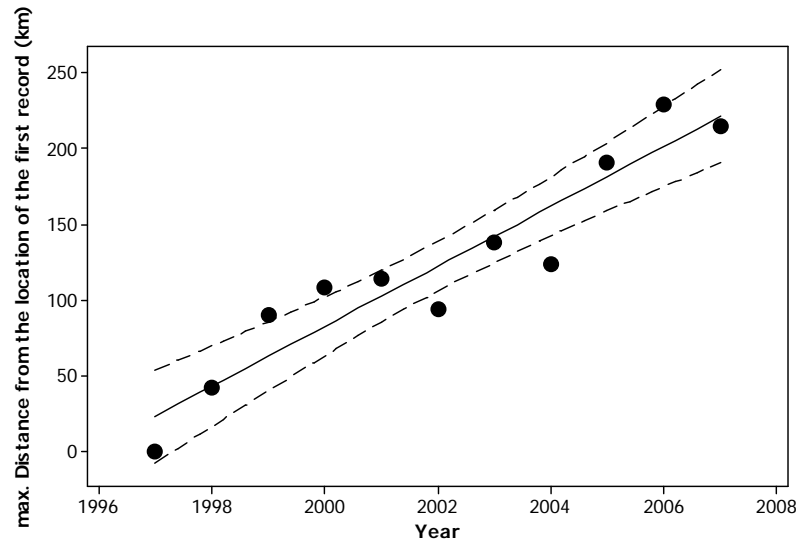

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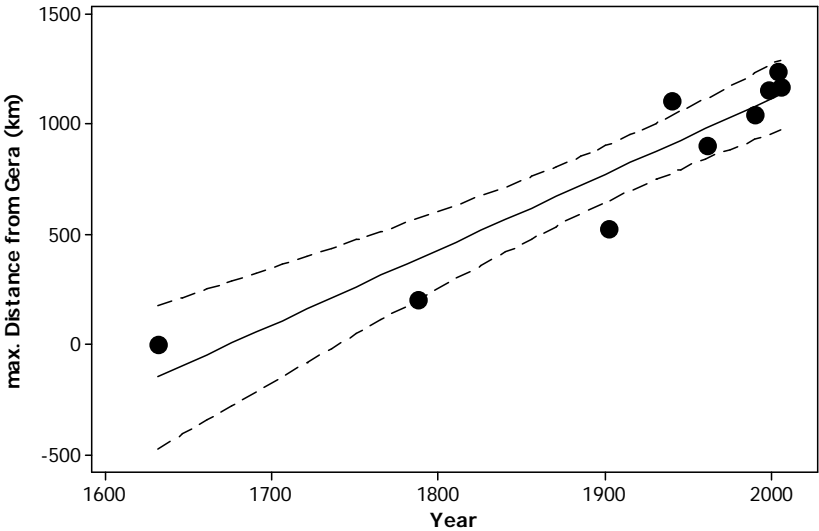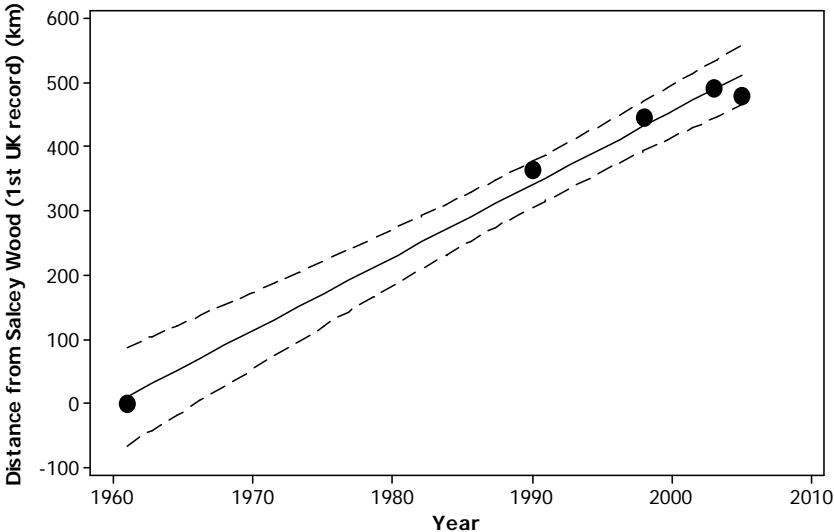768   c) *Aphelonyx cerricola*   d) *Andricus grossulariae*

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770

771 **Figure 3**.
772 **a)**

773
774 **b)**

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776 **c)**

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778