

Spatial and temporal dynamics in the development of invading cynipid communities in Britain

Tracey Begg



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Declaration

This thesis has been composed by me and is the result of my own work. It contains no work done in collaboration except where stated otherwise. The text does not exceed 100,000 words. No part of this thesis has been submitted to any other University in application for a higher degree.

Tracey Begg – November 2007

Abstract

The British Isles have been invaded by 12 alien cynipid gallwasps over the past 150 years. The first 4 of these species have been studied in depth and represent a model system in phytophagous insect community structure. In this thesis, I extend this research programme to incorporate 8 further invaders. I examine recent changes in the distribution of invading oak gallwasps in Britain and spatial patterns in the composition of the associated communities of phytophagous cynipid inquilines and parasitoids. I use fully quantitative webs to assess the diversity and strength of trophic interactions between native and invading species and assess the potential for apparent competition between gallwasps mediated by shared natural enemies.

Of the first 4 invaders to be studied, 3 have expanded their range since 1991/2. Three of these 4 species are now well established in Scotland, while *Andricus corruptrix* remains confined to England. Four new invaders (*A. aries*, *A. lucidus*, *A. grossulariae*, *Aphelonyx cerricola*) are established in southern England and are spreading. Rates of range expansion vary across species (between means of 3.3 and 24.4 km per year), and may be correlated with variation in lifecycles and abundance. The four newest invaders (*Neuroterus saliens*, *Plagiotrochus australis*, *P. coriaceus*, *P. quercusilicis*) are currently restricted to their sites of first record.

Previous studies on one of the early invaders, *Andricus quercuscalicis*, identified south to north and east to west declines in community species richness and in the abundance of specific parasitoid species. I find that: 1) Parasitoid associations with the asexual galls of *A. quercuscalicis* track inquiline recruitment to this host. 2) The longitudinal and latitudinal gradients in parasitoid species richness demonstrated in previous work are no longer apparent, suggesting that younger northern communities may be converging on their older southern counterparts. 3) Inquilines show increasing survivorship with distance from the original centre of their distribution in south east England, suggesting at

least temporary exploitation of enemy-free space. 4) The recently invading *Andricus* and *Aphelonyx* species have all rapidly recruited parasitoids and inquilines.

Fully quantitative webs were constructed for 4 sites in England and Scotland incorporating both native and invading cynipids. I tested the hypothesis that newly arriving gallwasp generations would fall within food web compartments based on their host oaks and location on the tree as demonstrated in previous work. Counter to this hypothesis, parasitoids attacking one of the newest invaders (*A. grossulariae*) break down host tree-associated compartmentalisation. Where *A. grossulariae* has yet to become established, host-based compartmentalisation remains pronounced. Despite extensive sharing of parasitoid species, I found only one strong indirect interaction between species (both aliens) and no evidence for widespread apparent competition.

Spatial density dependent predation on an appropriate scale can stabilise population dynamics. I quantified predation by blue tits (*Parus caeruleus*) of spring generation bud galls on Turkey oak (*Q. cerris*) at three spatial scales (shoots within branches, branches within trees, trees within sites). I found significant levels of bird predation, with most variation occurring between trees rather than between shoots within branches. Spatial density dependence was detected at sites in southern England, primarily at the level of trees within a site. Relationships at finer spatial scales were far more variable in magnitude and sign. My results suggest that blue tits forage primarily at the level of trees.

This thesis presents comprehensive new data on the establishment and spread of 12 invading cynipid species and on their interactions with native communities. The results further understanding of both spatial and temporal aspects of natural enemy recruitment to invading species. In particular, it is clear that individual invading species can significantly modify trophic linkage between established food web compartments. Finally, my data emphasise the significant (but often unstudied) contribution of highly mobile vertebrate predators to otherwise closed ecological microcosms.

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Chapter 1

General introduction

1.1 Introduction

Biological invasions represent natural, large scale perturbation experiments that allow the study of dynamic changes in community structure and function (Cornell and Hawkins, 1993; Schönrogge *et al.*, 1996). The study of biological invasions is fundamentally important because they currently represent a significant threat to global biodiversity, second only to habitat loss (Wilson, 1992). The monitoring of biological invasions is vital in order to understand the population dynamics, habitat tolerance and impact on native taxa of the invading species (Brown *et al.*, 2008). The consequences of introductions and invasions are numerous and in some cases, catastrophic (Moulton and Pimm, 1986; Townsend, 1996; Rodda *et al.*, 1999). In areas of high endemism, including Hawaii and Indonesia, the arrival of invading species has resulted in ecosystem collapse and extinctions of native species (Townsend, 1996; Simberloff *et al.*, 1997; Ricciardi *et al.*, 1998; Rodda *et al.*, 1999). Other potential consequences include the loss of ecosystem services such as pollination, natural pest control (Albrecht *et al.*, 2007; Kohler *et al.*, 2007) and a loss of productivity, for example, through reduced soil nutrient recycling where monocultures of invasive plants have eliminated endemic species (Griffiths *et al.*, 2005; Wilsey and Polley, 2006).

In Britain, a recent invader, the harlequin ladybird (*Harmonia axyridis*) has the potential to contribute to biotic homogenization (McKinney and Lockwood, 1999) and to negatively impact on up to 1000 species (Majerus, 2006). These are primarily insects (including non-target homoptera, alternative prey, members of

aphidophagous and coccidophagous guilds) and parasites, parasitoids, pathogens and symbionts of these species (Majerus, 2006).

Another potentially serious threat to biodiversity is global climate change which is predicted to cause range shifts by terrestrial temperate species towards higher latitudes and altitudes (Parmesan & Yohe 2003) where these species will invade resident, native communities as aliens (Walther *et al.* 2002). Although many studies illustrate the negative impacts of alien species on native food webs (e.g. Bradbury *et al.* 2001; Henneman & Memmott 2001), if aliens augment limiting resources for higher trophic levels they have the potential to ameliorate impacts of climate change.

My thesis concerns spatial and temporal patterns in the development of associated communities of natural enemies and other sources of mortality of 12 invading cynipid gallwasps (Hymenoptera: Cynipidae) in Britain. I will ask how the arrival of the most recent in a series of invaders to Britain has affected resident cynipid communities and, in particular, influenced the trophic links within these communities, mediated by natural enemies.

Cynipid galls are particularly useful for community studies. The larval stage is sessile and population density measurements are therefore accurate and relatively easy to obtain and each insect that enters a gall tends to leave a trace or remains that can be identified (Schönrogge, 1994).

Range expanding cynipids have proved valuable model systems for numerous studies on the pattern and process of biological invasions (Csóka *et al.*, 1997; Stone and Sunnucks, 1993; Stone *et al.*, 2001; 2002; 2007) and recruitment of communities of natural enemies (Hails and Crawley, 1991; 1992; Schönrogge *et al.*, 1994; 1996; 1998; 1999; 2000; Stone *et al.*, 1995; Hayward and Stone, 2005; 2006), the functional structures of communities (Askew, 1975; Askew and Shaw, 1986; Price and Pschorn-Walcher, 1988; Hoffmeister, 1992; Hoffmeister and Vidal, 1994; Mills, 1994; Stone *et al.*, 1995; 2002; Schönrogge and Crawley, 2000) and the development of communities (Cornell and Hawkins, 1993; 1994; Schönrogge *et al.*, 1995; 1996; 1998; 2000). These

studies will be discussed in the context of the relevant sections within this chapter (see sections 1.3 – 1.6).

In the following sections I provide an overview of cynipid biology and the natural enemies associated with cynipid galls, discuss ecological theory and the role of cynipids as an appropriate model system, describe the status of invading cynipid communities in Britain and discuss studies of cynipid community interactions in Britain. Finally, I will outline the major issues covered in each Chapter and acknowledge the contributions of collaborators to the work presented in this thesis.

1.2 Cynipid Biology

Cynipid gallwasps (Hymenoptera; Cynipidae, Cynipinae) constitute the second largest radiation of galling insects after the gall midges (Cecidomyiidae) (Ronquist and Liljeblad, 2001) with *c.* 1400 described species (Stone *et al.*, 2002). They are derived from parasitoid ancestors (Csóka *et al.*, 2005). Initially, cynipids induced galls on herbs and subsequently diversified into six recognised tribes. Five tribes are gall inducers (Aylacini, Diplolepidini, Pediaspidini, Eschatocerini, Cynipini) and one tribe consists of inquilines, phytophagous inhabitants of galls induced by other insects (Synergini) (Ronquist, 1994; 1999; Ronquist and Liljeblad, 2001; Csóka *et al.*, 2005). Around 10-15% of all cynipids cannot induce galls and develop as inquilines inside the galls of other cynipids (Ronquist, 1999; Nieves-Aldrey, 2001).

The oak host associations of Western Palaeartic gallwasps fall into three groups: those whose lifecycles involve two generations on oak species in section *Quercus sensu stricto*, those with lifecycles only involving oak species in section *Cerris*, and those whose lifecycles involve obligate alternation between these two sections (Folliot, 1964; Askew, 1984; Nieves-Aldrey, 1992; Stone and Sunnucks, 1993; Stone *et al.*, 2001; 2002; Cook *et al.*, 2002; Ács *et al.*, 2006). Host alternators are necessarily restricted to areas where oaks of both sections occur together, a fact that has had significant effects on geographical patterns in cynipid species richness in the Western Palaeartic (Stone *et al.*, 2002; Atkinson *et al.*, 2007). Because oaks in the

section *Cerris* were naturally restricted to southern regions of the Western Palaearctic (Iberia and north-western Africa, Italy, the Balkans, the Levant, Turkey and Iran), host alternating gallwasps were also naturally restricted to these regions. Oak gallwasp richness is thus much higher in these southern regions. For example, in central and southern Europe and the Balkans, 150 species have been recorded, compared with 56 species in northern Europe. Anthropogenic changes in the distributions of section *Cerris* oaks, however, have resulted in the large scale northwards shifts in distribution by multiple oak species that underlie this thesis (discussed in more detail in section 1.4 below).

The most species-rich gallwasp tribe, the oak gallwasps (Cynipini), have complex, cyclically parthenogenetic lifecycles and induce a wide variety of highly complex species- and generation-specific galls on oaks and other Fagaceae (Csóka *et al.*, 2005). Gall-inducing cynipids usually show strong fidelity to particular organs of their host plants, including flowers, leaves, buds, stems, twigs and roots, with only a small minority being able to induce galls on more than one organ. Oak cynipid galls support species-rich communities of organisms in addition to the gall inducer, including phytophagous inquilines, predators and parasitoids. Individual galls can contain many individuals of multiple species and constitute highly structured and ecologically 'closed' assemblages within which virtually all interactions are among a specific set of component species (Askew, 1961; 1984; Wiebes-Rijks and Shorthouse, 1992; Stone *et al.*, 2002). These assemblages are introduced in more detail in the following section.

1.3 Natural enemies of cynipid gallwasps

Chalcid parasitoid wasps

The natural enemies causing the highest degree of mortality in cynipid galls are chalcid parasitoid wasps (Hymenoptera, the superfamily Chalcidoidea) (Askew, 1984; Stone *et al.*, 2002). Six families of chalcids attack Western Palaearctic oak galls: Pteromalidae, Eurytomidae, Eupelmidae, Eulophidae, Ormyridae and

Torymidae (Askew, 1984; Stone *et al.*, 2002; Csóka *et al.*, 2005). Chalcids oviposit either close to or onto their host so larvae can feed either after prohibiting further growth by stinging (idiobionts) or as the host continues to develop (koinobionts) (Godfray, 1994; Hayward and Stone, 2005). Most chalcids reared from cynipid galls are solitary idiobiont ectoparasitoids that feed suctorially on their host (Askew, 1961; Schönrogge *et al.*, 1999; Schönrogge and Crawley, 2000). Chalcid species commonly attack a range of possible hosts inside the galls, i.e. gall formers and inquilines, but they also act as facultative hyperparasitoids and autoparasitoids attacking other chalcids of different or sometimes the same species (Askew, 1961; Askew and Shaw, 1974). Some exceptions to these rules include *Sycophila biguttata* and the gregarious *Baryscapus berhidanus*, both idiobionts (Askew, 1984; Schönrogge *et al.*, 1995). A range of parasitoid species are also at least partially herbivorous, feeding on gall tissues either before they feed on the host larva, for example, the phyto-entomophagous koinobiont, *Torymus cyanaeus*, or feeding on gall tissues as they move between host larvae within a single gall, for example, *Eurytoma brunniventris* (Askew, 1984).

The majority of chalcids exploit hosts in a wide range of oak gall types; few are restricted to just one oak gall type. Some chalcids that have broader host gall ranges over a wide geographical area can appear locally host gall specific. For example, *Aulogymnus skianeuros* in Britain (and probably over much of Western Europe) is specific to sexual generation galls of *Biorhiza pallida*, but in Eastern Europe it has also been reared from some 15 additional cynipid species, 9 of which also occur in Britain. *Aulogymnus trilineatus* is at the edge of its range and rare in Britain where it is known to attack only asexual generation *Andricus foecundatrix*, but on the continent it is recorded from a broad range of 29 types, 8 of which are found in Britain (Fulmek, 1968).

Most of the parasitoid species found in cynipid galls on oaks will not attack hosts even in cynipid galls on other plants, i.e. this community is relatively closed. However, a minority of species, such as *Eupelmus urozonus* and *E. vesicularis* (Eupelmidae), are exceptionally polyphagous and attack a range of endophytic hosts in a number of insect

orders (Askew, 1984). A few chalcid species also occasionally attack cynipid galls on plants other than oak (often *Rosa*) (Askew, 1984). For example, *Torymus flavipes*, *Eurytoma pistacina*, *Hobbya stenonota*, *Mesopolobus amaenus* and *Baryscapus pallidae* have also been recorded from rose galls of *Diplolepis mayri* (Pujade-Villar, 1992; Askew *et al.*, 2006). Some parasitoids, particularly eulophid species, are occasionally reared from oak galls despite being more generally associated with communities centered on leaf-mining hosts (e.g. *Cirrospilus* species, *Pediobius pyrgo*, *P. saulius*, *Closterocerus trifasciatus*, *Minotetrastichus frontalis*). However, these records appear to result from rare and opportunistic ovipositions as are those of a few ichneumonid (Ichneumonoidea) species that only occur sporadically (Fulmek, 1968; Hails *et al.*, 1990; Schönrogge *et al.*, 1996).

Inquilines

The word ‘inquiline’ is derived from the Latin *inquilinus*, meaning tenant or lodger (Hayward and Stone, 2005). Inquilines as strictly defined feed only on plant tissue and do not feed on the gall inhabitants directly. The major inquiline group in oak galls are cynipids in the tribe Synergini. These are probably derived from gall-inducing ancestors and have retained the ability to produce their own larval chambers lined with nutritive cells (Stone *et al.*, 2002; Csóka *et al.*, 2005; Hayward and Stone, 2005). However, they have lost the ability to induce galls *de novo* and feed obligately on (and to some extent stimulate the development of) plant tissues within developing galls (Shorthouse, 1980; Shorthouse and Rohfritsch, 1992). The presence of cynipid inquilines can be fatal for the gall former: some inquiline cynipids usually induce their cells either within the host gallwasp chamber or adjacent to it. Development of these chambers crushes the host cell and kills the gall inducer (Washburn and Cornell, 1981; Wiebes-Rijks, 1982; Askew, 1984; Shorthouse, 1993; Brooks and Shorthouse, 1997; 1998; Schönrogge *et al.*, 1998; 1999; 2000). Several inquilines can inhabit one gall and their presence can modify the overall size and shape of the gall (Shorthouse, 1980; Wiebes-Rijks, 1980).

Other groups occasionally considered to be inquilines are probably better regarded as gall predators, since they actively seek out and kill the gallwasp larva. Examples of this category include the larvae of a range of moths, particularly species in the genus *Pammene* which cause high mortality in some European *Andricus* galls (Schönrogge *et al.*, 1995), and the weevil *Curculio venosus*, which causes significant mortality in the sexual generation galls of the oak apple, *Biorhiza pallida* (Askew, 1965; Stone *et al.*, 2002; Csóka *et al.*, 2005).

Predators and other enemies

Gallwasps are also killed by predators, non-hymenopteran inquilines (see above) and herbivores. Opportunistic associates that can inflict high gallwasp mortality include herbivorous insect larvae such as butterflies, moths and sawflies which can consume young developing galls on leaves and flowers (Csóka *et al.*, 2005). Where such larvae cause serious defoliation of host plants, they may have a major influence on cynipid populations (Csóka *et al.*, 2005). An outbreak of a defoliating caterpillar resulted in the virtual extinction of three oak cynipids (all *Neuroterus spp.*) due to consumption or death of their leaf galls (Ejlersen, 1978; Csóka *et al.*, 2005).

Another class of predators that can induce high rates of mortality on gallers is birds. These include black-capped chickadees (*Parus atricapillus*) and the downy woodpecker (*Picoides pubescens*) which can cause up to 60% mortality in the galls of the Dipteran gall inducer *Eurosta solidaginis* (Diptera: Tephritidae) on *Solidago spp.* (Abrahamson *et al.*, 1989). Additional species of Paridae, notably blue tits (*Parus caeruleus*), peck open bud galls on *Q. cerris* in spring (Schönrogge *et al.*, 1998) and galls of *Cynips quercusfolii* on non-falling leaves (Wiebes-Rijks and Shorthouse, 1992). Nuthatches (*Sitta europea*) and great spotted woodpecker (*Dendrocopos major*) also extract gallwasps from their galls (Csóka, 1997). The high concentration of tannins in some galls is a deterrent to some predators, for instance, red deer (*Cervus elephus*) avoid browsing on acorns bearing knopper galls (Askew pers. comm.).

Emerged galls, particularly large woody ones, provide shelter for a menagerie of arthropods including mites, spiders, bugs, bark-lice, thrips, lacewings, wasps and ants. These facultative inhabitants of galls also support their own parasitoid assemblages, but because they are taxonomically distinct from those attacking gallwasps these can usually easily be identified.

1.4 Ecological theory and the role of cynipids as model systems

An important aim of community ecology is to understand the degree to which natural communities are structured by ecological processes such as competition for resources, predation or parasitism (van Veen *et al.*, 2006). The use of phytophagous insects in ecological studies is fundamentally important since, along with their host plants and natural enemies, these insects may constitute as much as 75% of all species and are abundant in all terrestrial ecosystems where plants are present (Strong *et al.*, 1984). One ecological process that may be involved in structuring such communities is interspecific competition for resources. However, many groups of phytophagous insects, including cynipids, have restricted and non-overlapping sets of host plants therefore the role of resource competition in these circumstances may be more limited (van Veen *et al.*, 2006). What may be of particular importance in these phytophagous insect communities are processes operating indirectly through shared natural enemies.

Apparent competition

Negative indirect interactions are thought to be relatively common and strong among endophytic insects, while direct competitive interactions are relatively less frequent between their sessile larval stages (Gilbert *et al.*, 1994; Holt and Lawton, 1993; 1994; Schönrogge *et al.*, in prep.). The results of negative indirect interactions, mediated by natural enemies have been called apparent competition (Holt, 1977). Apparent competition is defined as an indirect negative effect of one species on the population growth rate or abundance of another species, mediated through the action of shared natural enemies (Morris *et al.*, 2004).

Fully quantitative webs are a useful tool to describe community structure and identify the empirical evidence for apparent competition. Quantitative webs provide the clearest description of community structure, including data on all trophic links and associations expressed in the same units of density (Memmott and Godfray, 1994).

The oak cynipid community is an ideal model system to investigate empirical support for the existence of apparent competition using quantitative webs. As discussed, cynipid galls constitute highly structured and ecologically 'closed' assemblages within which virtually all interactions are among a specific set of component species (Askew, 1961; 1984; Wiebes-Rijks and Shorthouse, 1992; Stone *et al.*, 2002). The larval stage is sessile and population density measurements are therefore accurate and relatively easy to obtain and each insect that enters a gall tends to leave a trace or remains that can be identified (Schönrogge, 1994). The use of other model systems can be more problematic. Leafminers have been most frequently selected to investigate apparent competition (Memmott *et al.*, 1994; Rott and Godfray, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002) since like cynipids, the semi-permanent nature of the mine simplifies sampling. However, in one study, limits were drawn on the sets of species studied in order to make sampling feasible (Rott and Godfray, 2000). Restricting quantitative webs to only *Phyllonorycter* leafminers may have resulted in a lack of compartments in the web, compared with webs that include all potential leafminer hosts at a site. In my study, all cynipid species present at a site are included in the webs.

In field studies of phytophagous insects, short term apparent competition (within a generation) has been observed in aphid communities (Müller and Godfray, 1997; Morris *et al.*, 2001). Aphids were shown to suffer from apparent competition mediated by shared arthropod predators, but not primary parasitoids (Müller and Godfray, 1997; Rott *et al.*, 1998). However, in another study examining apparent competition between aphids mediated by a fungal pathogen, *Erynia neoaphidis* found no significant effects (Pope *et al.*, 2002). Only one field study successfully demonstrated the existence of apparent competition using quantitative webs involved

the experimental removal of two species of herbivore from a community of leaf-mining insects in a tropical forest (Morris *et al.*, 2004). The prediction that other species that share natural enemies with the two removed species experience lower parasitism and have higher population densities was fulfilled. In another field-based study, an aphid community was found to have some members of the community absent, despite the existence of suitable host plants around the sampling site and the common occurrence of these absent species in the aerial plankton (Müller *et al.*, 1999).

In the oak cynipid system, Schönrogge and Crawley (2000) investigated the effect of indirect interactions through shared natural enemies, in particular the potential for apparent competition (Holt, 1977; 1984; Holt and Lawton, 1993; 1994) using equivalent methods to those applied in similar studies on aphid and leaf-miner systems in which apparent competition appeared to play a major role (Müller *et al.*, 1999; Morris *et al.*, 2004). They found no indication that apparent competition via shared parasitoids and inquilines was a major factor affecting the dynamics of local cynipid communities. The recruitment of parasitoids and inquilines by invading cynipid species was therefore thought unlikely to have a strong effect on native cynipid species (Schönrogge *et al.*, 2006).

Population dynamics, predation and density dependence

In comparison with parasitoid attack, much less is known about the impact of predators such as birds on cynipids (Stone *et al.*, 1995; Plantard and Hochberg, 1996; Schönrogge *et al.*, 1996; 1999). The occasional superabundance of cynipid galls, particularly the invading species in Britain, suggests that they could potentially represent an important food source for birds.

Spatial density dependence is important because numerous studies have suggested that it can contribute to both the regulation and stability of predator-prey and host-parasitoid systems (Hassell, 1985; Hassell and Pacala, 1990; Hassell *et al.*, 1991; Redfern *et al.*, 1992; Hails and Crawley, 1992; Jones *et al.*, 1993; Schönrogge *et al.*,

1999; van Veen *et al.*, 2002; Matsumoto *et al.*, 2004). Spatial aggregation of deaths can have a stabilising effect on population dynamics if it creates a refuge which translates into temporal density dependence (Hassell, 1985). The refuge may result from increased mortality in patches of either low or high host density, or from heterogeneity in the risk of death which is density independent (i.e. associated with environmental factors other than local population density) (Hails and Crawley, 1992). The key point is that spatial density dependence must bring about temporal density dependence if it is to exert a regulatory influence on host population density (Hails and Crawley, 1992).

Compared with spatial density dependence, temporal density dependence is particularly difficult to detect. The length of time required to obtain a sufficiently long run of data together with annual variation in the rate of resource supply may make detection of density dependence difficult (Hails and Crawley, 1992). Environmental stochasticity may add further noise, obscuring temporally density dependent patterns, even when they are clearly present as spatially density dependent patterns within generations (Hassell, 1985). If measuring temporal density dependence is logistically difficult, meaningful interpretation of spatial density dependent relationships requires study at an appropriate spatial scale, i.e., that at which natural enemies recognise and respond to changes in host density (Hails and Lawton, 1983; Waage, 1983; Stephens and Krebs, 1987; Hails and Crawley, 1992). A hierarchical sampling scheme should allow us to infer at what spatial scale predators (or parasitoids) are acting.

Some evidence to support this theory from a study of *A. kollari* galls shows that a spatially density dependent pattern of attack of bud galls by birds could stabilise the invading populations by creating refuges in low density patches (Schönrogge *et al.*, 1999).

Detection of spatial density dependence requires a match between the spatial scale of sampling and that at which birds make foraging decisions (Connor *et al.*, 1999). Many studies show that insectivorous birds are able to detect highly rewarding food

patches, and forage preferentially in highly rewarding trees (Betts, 1955; Gibb, 1958, 1966; Krebs et al., 1977; Holmes and Schulz 1988; Naef-Daenzer *et al.*, 2000; Suhonen *et al.*, 1992). Positive spatial density dependence in tit exploitation of cynipid galls and other prey types has also been demonstrated between sites, reflecting variation in levels of gall exploitation in different bird populations (Itamies and Ojanen 1977; Schönrogge *et al.*, 1999). Less is known about spatial scales of foraging decisions within individual trees (Naef-Daenzer *et al.*, 2002). Most existing studies on tit foraging focussed on nest provisioning and used rates of caterpillar frass fall as a surrogate for caterpillar density, and this is difficult or impossible to estimate for specific branches within the same tree. Within-tree spatial scales can be examined, however, for galling insects and other endophytic prey where extraction leaves characteristic signs of bird predation (Connor and Beck 1994; Connor *et al.*, 1999; Schönrogge *et al.*, 1999). Studies of bird exploitation of leaf mining insects show that the sign of spatial density dependence reflects the ability of birds to handle prey: where birds find it difficult to extract multiple prey from a single leaf, spatial density dependence at this spatial scale is negative (Heads and Lawton 1983; Connor and Beck 1993; Connor *et al.*, 1999).

I examine the evidence for spatial density dependence in bird exploitation of alien *Andricus* galls on Turkey oak at three hierarchical spatial scales: branches within trees, trees within sites, and across 6 sites in the U.K. Previous work on tit foraging has also shown that foraging preferences for individual patches and prey types tracks changes in resource availability over timescales of days (Naef-Daenzer *et al.*, 2000, 2002; see also Gawlik (2002). At one site, I track the relationship between gall density abundance and signatures of density dependence through a single season. My *a priori* expectation is that any signature of density dependence will decline as total gall abundance declines, driving exploitation of alternative food resources (Connor *et al.*, 1999; Gawlik 2002).

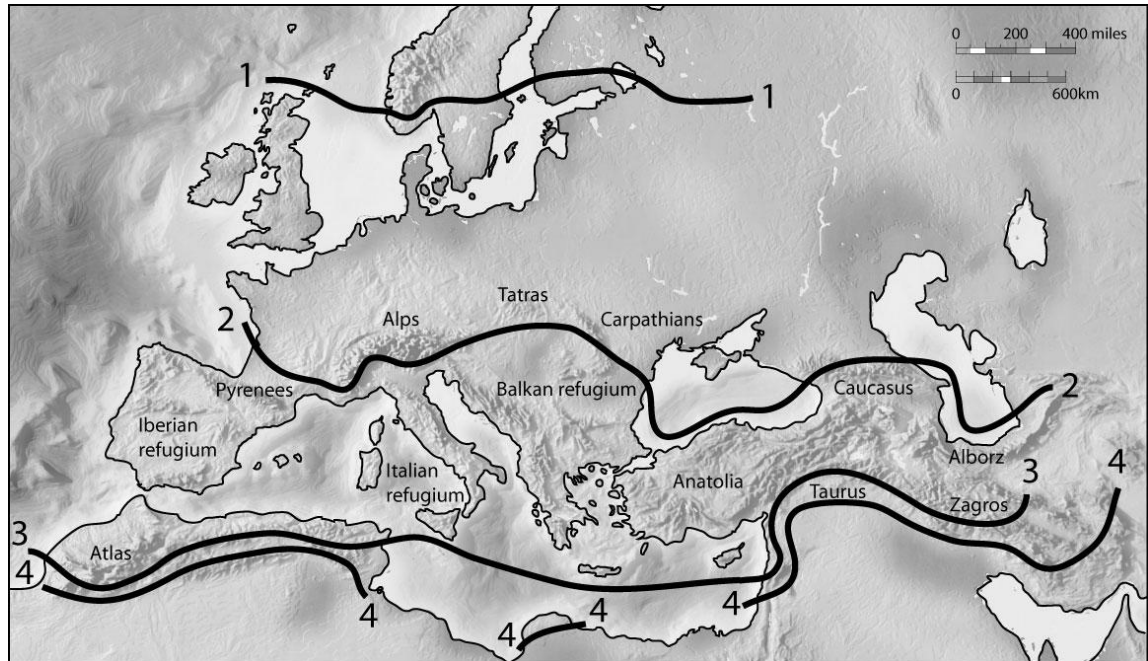
Invasion Biology

The discipline of invasion biology involves the study of introduced non-native species encompassing their ability to spread, their interactions with each other and with native species in receiving ecosystems. The geographic distributions of many non-native organisms have resulted as a direct consequence of human activity by either accidental or deliberate introductions of species beyond their native range. The distribution of these non-native species is constrained not by physiological limitations but more often by barriers that prevent dispersal. When such barriers are removed or crossed, naturally or via human intervention, populations may expand their distribution until new barriers to dispersal are reached (Carter and Prince, 1981; Crawley, 1986; Lawton, 1986; Stone and Sunnucks, 1993). In the case of host-alternating oak cynipids, the barrier preventing dispersal was the availability of an obligate host, Turkey oak *Quercus cerris*.

The natural distributions of all European section *Cerris* oaks correspond to some extent to glacial refugia for oaks during the Pleistocene ice ages. Figure 1.1 shows the regions of the Western Palaearctic occupied by the oak sections *Quercus sensu stricto* and *Cerris*.

Following the retreat of the ice sheets, only oaks in the section *Quercus* (particularly *Quercus robur* and *Q. petraea*) escaped these refugia and recolonised northern Europe (Stone *et al.*, 2001; 2007; Brewer *et al.*, 2002; Petit *et al.*, 2002; Csóka *et al.*, 2005). As a result, no cynipids dependent on *Q. cerris* (or any other section *Cerris* oak) for one or both generations in their lifecycle are native to northern Europe. However, over the last 400 years, *Q. cerris* has been planted extensively north and west of its native range, including Britain (Stone and Sunnucks, 1993; Stone *et al.*, 2002; 2007), creating a mosaic of *Q. cerris* patches within the natural distribution of section *Quercus sensu stricto* oaks thus providing suitable conditions for host-alternating gallwasps to complete their lifecycles. Figure 1.2 shows the current distribution of native and introduced *Q. cerris* across central Europe and Britain.

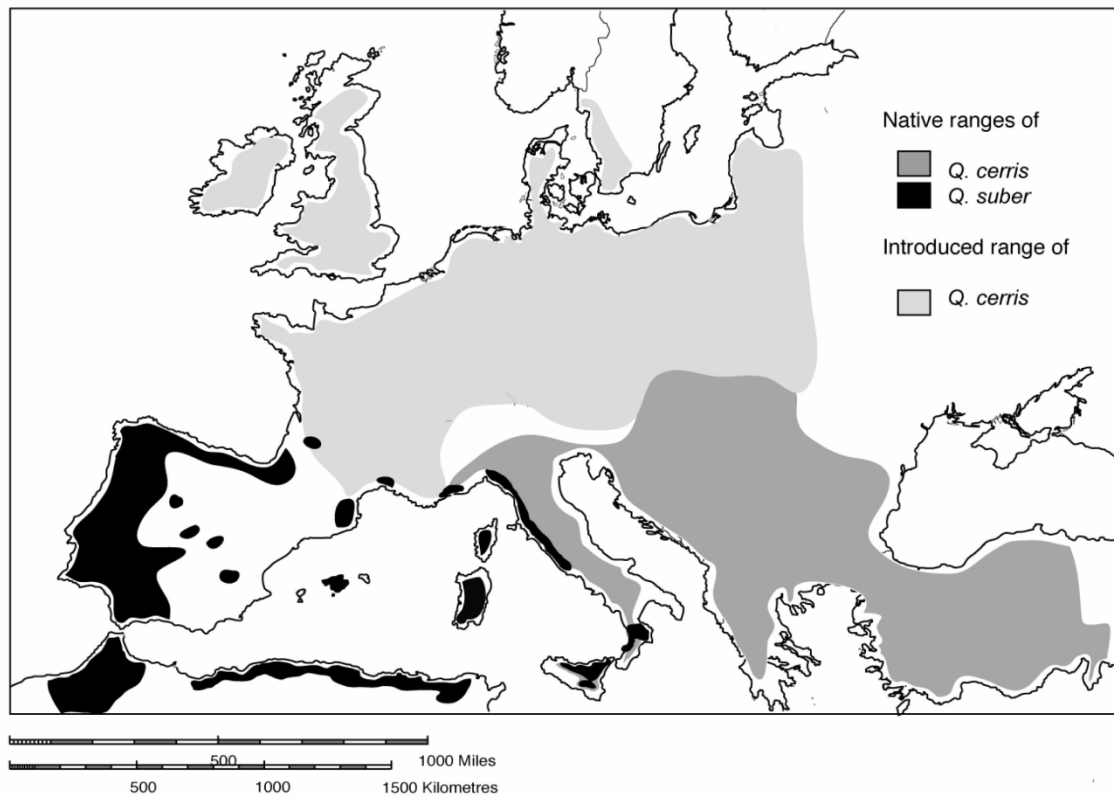
Figure 1.1 Regions of the Western Palaearctic occupied by the oak sections *Quercus sensu stricto* and *Cerris*. Only *Quercus s.s.* oaks are native between lines 1 and 2. Line 2 represents the northern limit of the natural distribution of section *Cerris* oaks. Oaks in section *Quercus s.s.* and *Cerris* are naturally found together between lines 2 and 3. Line 3 represents the southern limit of the oaks in the section *Quercus s.s.* Only section *Cerris* oaks are found between lines 3 and 4. Line 4 represents the southern limit of section *Cerris* oaks. Distribution sources are as follows: Europe (Tutin *et al.*, 1993), Turkey (Yaltirik, 1982; Davis, 1965-85), the former USSR (Konarov, 1936), Iran (Browicz and Menitsky, 1971), Iraq (Townsend and Guest, 1980), Palestine (Zohary, 1966).



The removal of the barrier preventing dispersal of host-alternating cynipids has facilitated the spread of the gallwasps to the north and west of their native range. This has allowed a rare opportunity to study the natural development of insect communities associated with these novel hosts as they move across the invaded range, particularly the extent to which natural enemies, principally parasitoid wasps, impact on cynipid communities.

Changes in host distributions over a range of spatial and temporal scales have the potential to leave subsets of natural enemies, such as parasitoids, behind allowing a host to enter 'enemy-free space' before sooner or later potentially being discovered and exploited. Enemy-free space was defined by Jeffries & Lawton (1984) as 'ways of living that reduce or eliminate a species' vulnerability to one or more species of natural enemies'.

Figure 1.2: The current distribution of native and introduced *Q. cerris* across central Europe and Britain



Across the invaded range of oak cynipids, there is the potential for enemy-free space to exist at different trophic levels within the oak cynipid community. The host plant *Q. cerris* may be free of cynipid infestation at the most northern and western limits of the invaded range of the tree. In areas where invading oak cynipids are found on *Q. cerris*, enemy-free space could exist where galls have not yet been exploited by either parasitoids or inquilines at the invasion front i.e. the northern or western limits of the invading ranges of these galls.

One factor which may affect the extent to which invading cynipid gallwasps gain enemy-free space is the origin of parasitoids attacking the cynipids. Parasitoids attacking cynipids or other insects within the gall may originate from the native range of the gallwasp and may be expanding their range by pursuit of the host cynipid across the invaded range. An alternative hypothesis, which is not mutually exclusive, is that parasitoids found attacking galls in the invaded range originate from the local parasitoid pool that have adapted to attack a novel cynipid host. From

an evolutionary perspective, this “host shift” route may play an important role in generating insect diversity by initiating host-race formation and speciation (Heard *et al.*, 2006). Phylogenetic (Janz and Nylin 1998; Janz *et al.* 2001), historical (Bush and Smith 1998; Carroll and Boyd 1992) and niche-breadth (Novotny *et al.*, 2002, 2003) data all imply that such host shifts are relatively common. Many authors have suggested that the existence of enemy-free space on novel hosts is an important factor permitting host shifts (Porter 1928; Bush 1974; Price *et al.*, 1980; Jeffries and Lawton 1984; Bernays and Graham 1988). However, field studies have provided little evidence of its frequency or importance (Heard *et al.*, 2006).

For oak cynipids, one study has given support for both pursuit and host shift hypotheses. A phylogenetic study indicated that the invading cynipid *A. kollari* has been pursued by populations of the parasitoid *Megastigmus stigmatizans* sharing the same native range and has also been exploited by host-shifting Iberian populations of the same species (Hayward and Stone, 2006).

1.5 Invading cynipid communities in Britain

Between 1830 and 1974 the native British oak cynipid fauna on *Quercus robur* and *Q. petraea* was invaded by four alien, host-alternating gallwasps native to south and eastern Europe: *Andricus kollari* (Smith, 1854), *Andricus quercuscalicis* (Claridge, 1962), *Andricus lignicolus* (Hutchinson, 1974) and *Andricus corruptrix* (Hutchinson, 1974). Work on the parasitoid communities associated with these first invaders is described in Section 1.4 below. More recently, three more alien host-alternating species, *Andricus lucidus* (Stone and Sunnucks, 1993), *Andricus aries* (Crawley, 1999), *Andricus grossulariae* (Walker, 2001) and one wholly dependent on *Q. cerris*, *Aphelonyx cerricola* (Leach and Shirley, 1999), have become established in Britain between 1990 and 2000.

Most recently, another four gallwasp species have reached Britain: *Neuroterus saliens* (Redfern, 2006), which is wholly dependent on *Q. cerris*, and three *Plagiotrochus* species, *P. australis* (Robbins, 2007), *P. coriaceus* (Robbins, 2007)

and *P. quercusilicis* (Hancy and Hancy, 2004) have been recorded from *Q. ilex*. There are very few records for these four species and *P. australis* and *P. coriaceus* were first recorded only in 2007, after completion of data collection for this study. None of the four species are therefore included in analyses within this thesis. It remains to be seen whether these species will join the list of established invaders in Britain.

History of the invasions

The invasion of Britain by Andricus kollari, Andricus lignicolus and Andricus corruptrix

The first group of invading cynipids (*A. quercuscalicis*, *A. kollari*, *A. lignicolus*, *A. corruptrix*) invaded Britain over the last 175 years (Schönrogge *et al.*, 1996; 1998; Walker *et al.*, 2002). The invasion of north west Europe by these species (except *A. kollari*) (Stone *et al.*, 2007), is thought to have occurred entirely without direct human assistance (Stone *et al.*, 2007). The invasion histories of these species have previously been described in detail (Stone *et al.*, 1995; 2007; Schönrogge *et al.*, 1998; Walker *et al.*, 2002).

The annual lifecycles of these four host-alternating species involve a sexual generation on *Q. cerris* in the spring and an asexual generation on *Q. robur* and *Q. petraea* in the autumn (the asexual generation of *A. quercuscalicis* is restricted to *Q. robur* and its hybrid with *Q. petraea*, *Q. rosaceae*). The sexual generations of *A. kollari*, *A. lignicolus* and *A. corruptrix* induce small bud galls that are very similar in size and structure. *Andricus quercuscalicis* induces small sexual galls on the catkins of *Q. cerris* and so-called knopper (asexual) galls on the acorns of *Q. robur* in the autumn (Figure 1.3). The asexual generations of *A. kollari*, *A. lignicolus* and *A. corruptrix* all form on the buds of either *Q. robur* or *Q. petraea*.

Andricus kollari was imported to Britain from the eastern Mediterranean (Stone *et al.*, 2007) as galls were a raw material for wool dyeing and ink industries in Devon

around 1830 (Parfitt, 1856; Lindley and Moore, 1870; Walker *et al.*, 2002). Escaping adults were recorded in 1834 (Smith, 1854; Walker *et al.*, 2002) and by 1871, *A. kollari* was recorded in Scotland (Hardy, 1871; Trail, 1872; 1878; 1882; Cameron, 1874; 1878). *Andricus kollari* is now widely distributed throughout Britain, including islands fringing the west coast of Scotland (Wormell, 1982; Walker *et al.*, 2002), Caithness and Sutherland in northern Scotland (Begg, pers. obs.) and also Orkney (G. Stone, pers. comm).

Andricus lignicolus and *A. corruptrix* were first reported in West Sussex in 1972 (Hutchinson, 1974). *Andricus lignicolus* spread rapidly and had reached Scotland by the late 1980's (Walker *et al.*, 2002), now being found as far north as Sutherland in northern Scotland (see Chapter 4). The spread of *A. corruptrix* in Britain has been slower. The few records available suggest it is distributed thinly and patchily (Walker *et al.*, 2002). It is also possible that this gall is under-reported: both generations are cryptic, particularly in the younger stages. The sexual bud gall on *Q. cerris* could be confused with the morphologically similar bud galls of *A. kollari* or *A. lignicolus*, while the asexual galls are similar in colour, texture and size to an oak bud. Figures 1.3 and 1.4 show those invading cynipid galls featured in this study.

Information about parasitoid recruitment in these three species following their arrival in Britain is sparse compared with *A. quercuscalicis* (discussed below). The parasitoid assemblages associated with these three species are discussed in detail in Chapter 2.

The invasion of A. quercuscalicis in Britain

Of the first 4 cynipids to invade Britain, *A. quercuscalicis* has been most extensively studied. I will therefore describe the invasion history of *A. quercuscalicis* in detail, including a review of studies of parasitoid recruitment to the galls in Britain. The invasion history of *A. quercuscalicis* across its native and invaded range in Europe is described in Chapter 3 (see Discussion). The first record for *A. quercuscalicis* was from East Anglia in 1958 (Claridge, 1962). This gallwasp then spread throughout most of England and Wales and was recorded for the first time in Scotland in 1993 (Schönrogge *et al.*, 1998). Detailed studies of *A. quercuscalicis* populations in

Britain have been carried out since 1979 (Collins *et al.*, 1983; Hails *et al.*, 1990; Hails and Crawley, 1992; Stone and Sunnucks, 1993; Schönrogge *et al.*, 1994; Stone *et al.*, 1995).

(i) The asexual generation

In Britain, the asexual galls of *A. quercuscalicis* were virtually free of parasitoid attack for about 25 years after the gall was first reported (Collins *et al.*, 1983; Hails and Crawley, 1990). Parasitoids were recorded in the late 1970's, with slow recruitment for about 10 years thereafter. The first parasitoids reared from the asexual knopper galls were *Torymus cyanaeus* and *Mesopolobus amaenus* (Hails and Crawley, 1990). Interestingly, *T. cyanaeus* has not been reared from *A. quercuscalicis* since. *Mesopolobus amaenus* attacked both the gall former and inquiline soon after their appearance in asexual knopper galls, but has since remained rare (Schönrogge *et al.*, in prep). *Mesopolobus amaenus* may represent an early successional species in community development in Britain and was also the only parasitoid recorded from Irish galls during the first survey of the species in Ireland in 1994/5 (Schönrogge *et al.*, 1995).

A striking feature of the last survey of the knopper gall community in 1991/2 was the rapid increase in inquiline cynipid abundance over the period 1990 - 1995, particularly in south east England (Schönrogge *et al.*, 1996), a trophic group previously absent from British populations (Martin, 1982; Hails *et al.*, 1990; Schönrogge *et al.*, 1996). By 1995, inquilines were present in high densities across south east England. This development triggered a change in the species composition and abundance of the associated parasitoid assemblage, because some parasitoid species preferentially attack inquilines. Parasitoid recruitment had also followed the invasion route of the host (Schönrogge *et al.*, 1995; 1996). By 1995, the species composition of the parasitoid assemblage associated with knopper galls in Britain contained a subset of those recorded in the native range of the gallwasp, continuing a trend seen across Europe from the native range to the British Isles (Schönrogge *et al.*, 1995; 1996; Stone *et al.*, 1995). The composition and species richness of the

parasitoid and inquiline community in Britain and across Europe is discussed in depth in Chapter 3.

Although parasitoid species richness was lower in Britain, the parasitoid species identity in native range and invaded range within Britain were similar (Schönrogge *et al.*, 1996). The convergence of the parasitoid faunas in the invaded and native ranges, despite differing environmental conditions and resident cynipid faunas, suggests a deterministic link between gall attributes (e.g. host tree species, phenology, the plant organ galled, gall morphologies) and parasitoid community composition, species richness and abundance (Schönrogge *et al.*, in prep.).

Schönrogge *et al.* (1996) predicted that should the range of *A. quercuscalicis* expand across Britain, inquilines would eventually follow the pattern of range expansion, then parasitoids, attacking their inquiline hosts. This and alternative hypotheses concerning parasitoid community development in *A. quercuscalicis* in the invaded range are considered fully in Chapter 3 (see Discussion).

(ii) The sexual generation

As with the asexual generation, the parasitoid assemblages recruited to the sexual generation of *A. quercuscalicis* represented a subset of those recorded in Europe (Stone *et al.*, 1995; Schönrogge *et al.*, 2006). Recruitment of parasitoids to the sexual generation galls differed to the asexual generation in that there was much less of a time lag between host arrival and parasitoid attack. Several hypotheses for this difference are postulated in Chapter 4 (see Discussion).

The galls of the sexual and asexual generations of *A. quercuscalicis* differ in several respects. The galls are morphologically and phenologically very different (see Figures 1.3 and 1.4). The sexual gall is only 1-2 mm long, thin-walled, and develops very rapidly on the catkins of *Quercus cerris* (Schönrogge *et al.*, 1996) while the asexual generation gall has a thick woody wall, reaches a diameter of up to 20mm, and develops over several months on the acorns on *Q. robur* (Schönrogge *et al.*, in

prep.). These differences have two major consequences for the associated communities. The asexual generation galls develop through a clear sequence of structural stages and the parasitoids attacking this generation form a successional series associated with increasing host size from small parasitoid species with short ovipositors to larger species with long ovipositors (Schönrogge *et al.*, 1995; Schönrogge *et al.*, in prep.). In contrast, the rapid development of the sexual generation galls prevents such temporal structuring of parasitoid attack. Also, the asexual generation galls are attacked by several inquiline *Synergus* species, while the far smaller sexual generation galls never harbour inquilines, because of their size or perhaps because they develop too rapidly to allow development of secondary inquiline larval chambers (Schönrogge *et al.*, in prep.).

Although the galls of both generations of *A. quercuscalicis*, at least in the south east of England, are consistently attacked by a set of parasitoid species at sometimes high levels, only one parasitoid species (*Cecidostiba fungosa*) is common to the communities of both generations and occupies a different role in each, attacking the gall former in the small catkin gall, and inquilines in the large knopper acorn gall (Schönrogge *et al.*, 2006). The lack of a tight link between the population dynamics of any parasitoid species and the host might explain why parasitoids, even with high attack rates, do not appear to regulate host populations. In fact, attack rates on the gallwasp in the asexual gall were reported in 1996 to be only 0.2% in the UK, while attack rates in France, Belgium and the Netherlands were 8% - 13% (Schönrogge *et al.*, 1996). *Megastigmus stigmatizans*, the parasitoid largely responsible for this higher level of mortality on the continent, was very rare in Britain in the mid 1990's: although it was detected in rearings of ~40,000 knopper galls in the UK (Schönrogge *et al.*, 1995), it was not abundant enough to be detected during dissections of 1050 galls (Schönrogge *et al.*, 1996). One might predict that this species is most likely to increase in abundance, inducing greater mortality, in British *A. quercuscalicis* populations over time.

Figure 1.3: Photographs showing known sexual generations of invading cynipid galls in Britain included in this study.



Andricus lucidus



Andricus grossulariae



Andricus quercuscalcis



Andricus kollari



Andricus lignicolus



Andricus corruptrix

Figure 1.4: Photographs showing asexual generations of invading cynipid galls in Britain included in this study. *Aphelonyx cerricola* is the exception, having only one known generation.



Andricus corruptrix



Andricus lignicolus



Andricus kollari



Andricus lucidus



Andricus aries



Andricus grossulariae



Aphelonyx cerricola



Andricus quercuscalicis

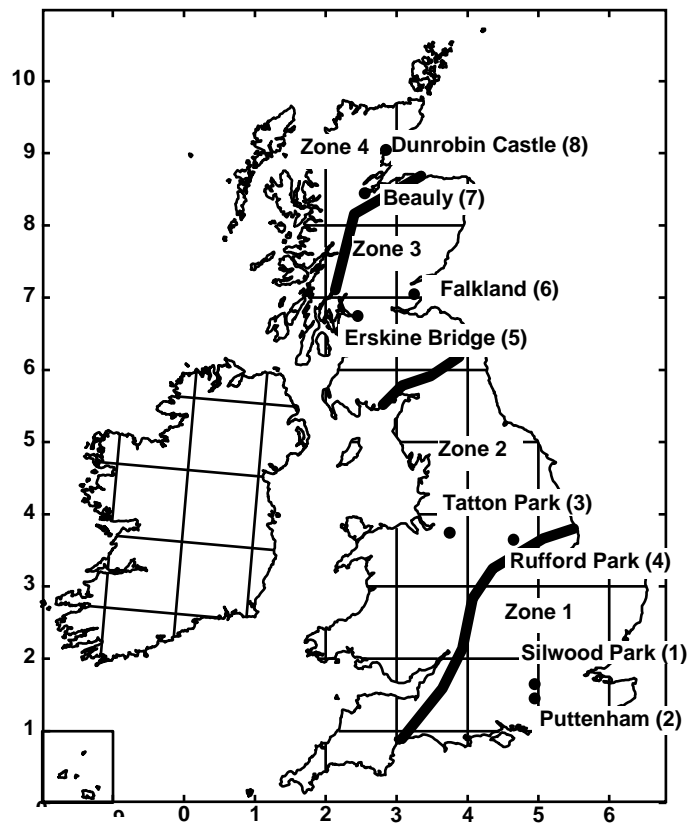
The changing status of cynipid communities in Britain

In 1996, the first group of invaders (*A. quercuscalicis*, *A. kollari*, *A. lignicolus* and *A. corruptrix*) were at different stages in their invasion of Britain resulting in variation in invader species richness across the country. Schönrogge *et al.* (1996) identified 4 geographical zones based on the number of alien cynipid species present (Figure 1.5), extending from all four in Zone 1 in south eastern England, to 3 in Zone 2 (no *A. corruptrix*), 2 in Zone 3 (additional loss of *A. quercuscalicis*) and only *A. kollari* in the northernmost Zone 4, which includes northern Scotland (Schönrogge *et al.*, 1996; 1998; 1999).

Since Schönrogge' *et al.*'s study, significant changes have occurred in the distribution and diversity of cynipid galls within Britain. Eight new invading cynipid species have been recorded in Britain and in the course of this thesis, it will be shown that the more established invaders (*A. quercuscalicis*, *A. lignicolus*, *A. corruptrix*) have continued range expansion both north and west of the ranges recorded in previous studies.

The distribution and parasitoid assemblages of four of the new invading species (*A. aries*, *A. lucidus*, *A. grossulariae* and *Aphelonyx cerricola*) in Britain are largely unknown to date. Sporadic distribution records exist for each of the four species (Crawley, 1997; Shirley, 1998; Wurzell, 2000; Walker, 2001; Walker *et al.*, 2002), principally from the south east, including west London and Berkshire (possibly as a consequence of increased sampling effort in these areas, or perhaps because they are closest to the continental origin of the species as was also the case for *A. corruptrix*, *A. lignicolus* and *A. quercuscalicis*). The current distribution of these four new species will be discussed fully in Chapter 2.

Figure 1.5: Geographical locations of the eight sample sites used in the 1994 and 1995 collections. The thick lines indicate the boundaries of the four zones according to the 1994/95 distribution of the invading gallwasps. Study sites used during previous studies are numbered 1-8 (Schönrogge *et al.*, 1998; 1999; Schönrogge and Crawley, 2000).



1.6 Contents of this thesis

In this thesis, I examine several aspects of the ecology of invading cynipid communities in Britain, including: (1) the current distribution, guild structure and species composition of invading cynipid communities (2) the impact of invading cynipids on existing cynipid communities in Britain, and (3) the importance of bird predation on cynipid mortality. I use this model system to explore ecological themes including apparent competition, community structure and interaction and density dependence.

In Chapter 2, I describe the current distributions in Britain of the 8 invading cynipid species included in this study. For the 8 invading cynipids established in Britain

prior to this study (*A. quercuscalicis*, *A. kollari*, *A. lignicolus* and *A. corruptrix*), this chapter serves to update current published distribution information. For the 4 more recently invading species studied (*A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*), this chapter provides the first British distribution maps for these species. Additionally, the parasitoid assemblages of these 4 recent invaders will be described, providing the first baseline data of the parasitoid communities associated with these cynipids at a very early stage of their invasion in Britain. Comparisons will also be made with the invasion histories (both distribution and community composition) of the more established set of invaders, particularly with the way in which the community associated with *A. quercuscalicis* has developed and changed over time.

In Chapter 3, I examine aspects of temporal and spatial patterns in the recruitment of parasitoids and inquilines to *A. quercuscalicis* following continued range expansion by this species across the north and west of Britain over the last 10 years. I evaluate the current geographical distribution of parasitoid and inquiline recruitment in the asexual generation, comparing species abundance, richness and diversity from south/north and east/west transects across Britain. I will test the prediction that should high inquiline abundance follow *A. quercuscalicis* range expansion, the same patterns of increased inquiline and parasitoid species richness noted by Schönrogge *et al.* (1996) will follow. In addition, I will test the hypothesis that the parasitoid community of the asexual galls in the invaded range is continuing to converge on that of the native range with increasing residence time of *A. quercuscalicis* in Britain. I will also look for evidence of enemy-free space at the invasion front of each trophic level of invading cynipid communities.

In Chapter 4, I compare quantitative webs for a guild of multiple native and 4 invasive cynipid gallwasps (*A. quercuscalicis*, *A. lignicolus*, *A. kollari*, *A. corruptrix*) that has recently been invaded by 4 more alien cynipids from Europe (*A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*). I examine changes in community structure and function that may have resulted as a consequence of the arrival of these additional invading alien cynipids. By comparing data before and after the arrival of a second group of 4 invaders I will ask the following questions: (1) Have attack rates

for parasitoids of invading gall wasps changed over the last 10 years? (2) Has the arrival of new invasive species altered the extent to which parasitoid communities focused on native and invading gallwasps interact? (3) Is apparent competition currently important in structuring the cynipid communities?

Through these questions, I will test the following hypotheses:

- That web complexity will reflect the residence times of the invaders where they are sampled. This pattern was demonstrated for *A. quercuscalicis* on a European scale by Schönrogge *et al.* (1995), and for the same species in the UK by Schönrogge *et al.* (1996). In general, this hypothesis predicts fewer trophic links in northern than southern Britain.
- That shared parasitoids will place the 4 more recent invaders in food web compartments containing other gallwasp generations on the same host oaks. This is based on previous studies showing that parasitoid communities associated with *Q. cerris* are qualitatively and quantitatively distinct from those associated with *Q. petraea* and *Q. robur* (Schönrogge and Crawley, 2000).

In Chapter 5, I investigate the importance of bird predation as a factor affecting mortality of cynipids that form bud galls on *Q. cerris* in spring. I test the hypotheses that bird predation of bud galls is spatially density dependent and as such, that birds could exert a degree of population regulation or control of cynipid populations (Schönrogge *et al.*, 1999).

In Chapter 6, I discuss my findings in the context of the general ecological issues raised in this first chapter, and suggest rewarding and important avenues for future work.

1.7 Contributors to the content of this thesis

Data collected for webs from southern Britain (Puttenham Common and Silwood Park) in Chapter 5 was collected on my behalf by Karsten Schönrogge and field assistants from CEH Dorset and thereafter reared and identified by me. Some initial analyses for the east to west transect in Chapter 3 were carried out by my undergraduate project student, Chloe Bellamy. All analyses presented here are my own work. Identification of voucher specimens were confirmed by expert taxonomists of parasitoids (Dr. R. R. Askew, UK) and cynipid inquilines (Dr. G. Melika, The Plant Protection and Soil Conservation Service of County Vas, Hungary).

Chapter 2

The current distribution of invading cynipids in Britain and the status of their associated communities

2.1 Introduction

Biological invasions have generated considerable interest as ecological phenomena for decades (Sakai *et al.*, 2001). Natural communities are under constant threat from invasive organisms. Invasion can result from natural range expansion, or can be facilitated by anthropogenic means (Aebi *et al.*, 2007). Often there are few records for a given species during the early stages of an invasion, yet this stage is of major interest because it is the period over which biotic interactions with native communities of competitors, prey and natural enemies become established. Because their galls provide evidence of the arrival of novel species, gallwasps (including the pest chestnut gallwasp *Dryocosmus kuriphilus*; Aebi *et al.*, 2006) provide many well-studied examples of this key early stage of the invasion process.

Invading alien oak gallwasps became established in Britain due to the introduction of an obligate host, Turkey oak (*Quercus cerris*). *Quercus cerris* was grown for use in wainscoting and ornamental purposes across Europe (Spoltiswoode, 1842; Walker *et al.*, 2002). The native range of *Q. cerris* is restricted to central and south-eastern Europe, but over the last 400 years, *Q. cerris* has been planted extensively north and west of its native range, including Britain (Stone and Sunnucks, 1993; Stone *et al.*, 2002b; 2007), creating a mosaic of *Q. cerris* patches within the natural distribution of section *Quercus sensu stricto* oaks. This mosaic has allowed range expansion by

multiple species whose lifecycles require host alternation between these two oak groups (see Chapter 1).

Quercus cerris is found throughout Britain, although it much less common in Scotland (Figure 2.1). North of central Scotland, plantings are typically isolated and restricted. Regeneration of *Q. cerris* is limited in Scotland, particularly north of central Scotland, but is localized to widespread elsewhere. Most *Q. cerris* in northern Scotland are over 100 years old and many of the oldest specimens are in decline (Walker *et al.*, 2002).

Figure 2.1 The distribution of Turkey oak (*Quercus cerris*) in Britain showing 10 km squares in red where the species is present (Preston *et al.*, 2002).



Between 1830 and 1974, the native British oak cynipid fauna on *Quercus robur* and *Q. petraea* was invaded by four alien, host-alternating gallwasps native to south and eastern Europe: *A. kollari* (Smith, 1854), *A. quercuscalicis* (Claridge, 1962), *A. lignicolus* (Hutchinson 1974) and *Andricus corruptrix* (Hutchinson, 1974). More

recently, three more alien, host-alternating species, *Andricus lucidus* (Stone and Sunnucks, 1993), *Andricus aries* (Crawley, 1999), *Andricus grossulariae* (Walker, 2001) and one wholly dependent on *Q. cerris*, *Aphelonyx cerricola* (Leach and Shirley, 1999), have become established in Britain between 1990 and 2000. The lifecycles of these 8 species are described in Chapter 1 (Section 1.5).

Most recently, another four gallwasp species have reached Britain: *Neuroterus saliens* (Redfern, 2006), which is wholly dependent on *Q. cerris*, and three *Plagiotrochus* species, *P. australis* (Robbins, 2007), *P. coriaceus* (Robbins, 2007) and *P. quercusiliis* (Hancy and Hancy, 2004) have been recorded from *Q. ilex*. These four newest invaders are known only from their sites of first record (Table 2.1) as recently as 2007. None of the four species were recorded in the surveys described in this Chapter. Documented first records for each of these 12 invading cynipids are shown in Table 2.1.

Table 2.1 Documented first records for invading cynipid species in Britain. *Andricus lucidus* (as its sexual generation, known as *A. aestivalis*) was recorded in Britain as an isolated record from Loch Lomond by Cameron (1893), but cannot be regarded as established in the British fauna prior to recent times.

Species	Documented year of 1 st record	Location	Author and publication date
<i>Andricus kollari</i>	1834	Devon	Smith (1854)
<i>Andricus quercuscalicis</i>	1962	East Anglia	Claridge (1964)
<i>Andricus lignicolus</i>	1972	West Sussex	Hutchinson (1974)
<i>Andricus corruptrix</i>	1972	West Sussex	Hutchinson (1974)
<i>Andricus lucidus</i>	1992	Richmond, London	Stone and Sunnucks(1993)
<i>Andricus aries</i>	1997	Maidenhead, Berkshire	Crawley (1999)
<i>Aphelonyx cerricola</i>	1999	Hampstead, London	Leach and Shirley (1999)
<i>Andricus grossulariae</i>	2001	Greater London	Walker (2001)
<i>Plagiotrochus quercusiliis</i>	2004	Eden project, Cornwall	Hancy and Hancy (2004)
<i>Neuroterus saliens</i>	2006	Hackney, London	Redfern (2006)
<i>Plagiotrochus australis</i>	2007	Glamorgan, Wales	Robbins (2007)
<i>Plagiotrochus coriaceus</i>	2007	Glamorgan, Wales	Robbins (2007)

The first group of invading cynipids (*A. corruptrix*, *A. kollari*, *A. lignicolus*, *A. quercuscalicis*) invaded Britain over the last 175 years (Schönrogge *et al.*, 1996; 1998; Walker *et al.*, 2002). The invasion of north western Europe by these species (except *A. kollari*, see Chapter 1, Section 1.5) is thought to have occurred entirely without direct human assistance (Stone *et al.*, 2007). The invasion histories of these species have previously been described in detail (Stone *et al.*, 1995; 2007; Schönrogge *et al.*, 1998; Walker *et al.*, 2002) and are discussed in Chapter 1 (see Section 1.5).

In 1996, the first group of invaders (*A. corruptrix*, *A. kollari*, *A. lignicolus*, *A. quercuscalicis*) had spread across Britain to different degrees, resulting in variation in invader species richness across the country. Only *A. kollari* was distributed throughout Britain (Wormell, 1982; Walker *et al.*, 2002), and Schönrogge *et al.* (1996) identified four geographical zones based on the number of invading cynipid species present (see Chapter 1, Figure 1.5).

Since Schönrogge *et al.*'s study, significant changes have occurred in the distribution and species richness of cynipid galls within Britain. Eight new invading cynipid species have been recorded in Britain (Table 2.1). The distribution and associated parasitoid assemblages of the 4 best established of the new invading species (*A. aries*, *A. grossulariae*, *A. lignicolus* and *Aphelonyx cerricola*) in Britain are largely unknown to date. Sporadic distribution records exist for each of the four species (Crawley, 1997; Shirley, 1998; Wurzell, 2000; Walker, 2001; Walker *et al.*, 2002), principally from the south east, including west London and Berkshire.

In this Chapter, I describe the current distributions in Britain of the 8 invading cynipid species surveyed for this study. For the 4 invading cynipids established in Britain prior to this study (*A. quercuscalicis*, *A. kollari*, *A. lignicolus* and *A. corruptrix*), this chapter serves to update current published distribution and community information. For the 4 more recently invading species studied (*A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*), this chapter provides the first British distribution maps for these species. The first cynipid species to invade

Britain, *A. kollari*, is now widespread. The remaining 7 species in the studied group share the same dependence on *Q. cerris*, either as the sole oak host (*Aphelonyx*) or as one host in an alternating lifecycle (the *Andricus* species), and are native to the same regions in southern Europe. It is thus likely that all of them will continue to expand their ranges across Britain, becoming widespread throughout the country over time.

The parasitoid and inquiline communities associated with these 4 recent invaders will also be described, providing the first baseline data for this early stage of their invasion in Britain. I compare observed communities for these galls with those in their native range, and compare their invasion histories and parasitoid communities with data for the first four invaders, particularly *A. quercuscalicis*. If enemy recruitment in these new invaders parallels *A. quercuscalicis* (see Chapter 1, Section 1.5), their short residence time in Britain (up to 15 years) predicts no attack by either parasitoids or inquilines.

2.2 Methods

2.2.1. Collection, rearing and identification of invading galls in Britain

In the autumn and spring of 2004 and 2005, a country-wide survey of the 8 species of invading galls included in this study (*A. aries*, *A. corruptrix*, *A. grossulariae*, *A. kollari*, *A. lignicolus*, *A. lucidus*, *A. quercuscalicis* and *Aphelonyx cerricola*) was made to determine the current distribution of each of the species across Britain. Visits were made to potential collection sites including public parks, private estates, golf courses, cemeteries, woodland and hedgerows; all approximately 50 km apart across Britain (see Appendix Table 7.1). Where suitable tree species were found (*Quercus robur*, *Q. petraea*, *Q. cerris*), sites were searched for 1 hour and all galls of invading cynipids with the exception of *A. quercuscalicis* were collected and reared. *Andricus quercuscalicis* was superabundant at many sites, and only presence or absence was recorded. This species was sampled using an alternative transect sampling design, described in Chapter 3.

All rearings were stored in an outside insectary and emerging adult gallwasps, inquilines and parasitoids were collected weekly and parasitoids were identified using appropriate keys (Askew and Thúroczy, in prep; Pujade-Villar *et al.*, in prep). Sub samples of parasitoid species were sent to Dr R. R. Askew (UK) to confirm correct and consistent identification. Inquiline identification is difficult, and all inquilines were therefore sent for identification by a specialist taxonomist (Dr. G. Melika, The Plant Protection and Soil Conservation Service of County Vas, Hungary).

2.3 Results

2.3.1. Invading cynipid distributions in Britain

The current distributions of the 8 invading cynipid species are shown in Figures 2.2 and 2.3. The first 4 invading species (Figure 2.2: *A. corruptrix*, *A. kollari*, *A. lignicolus*, *A. quercuscalicis*) have a more widespread distribution across Britain than the 4 more recent arrivals, first recorded in Britain after 1992 (Figure 2.3: *A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*). Both *A. kollari* and *A. lignicolus* are widespread extending across north east Scotland, but were absent from large areas of north west Scotland. *Andricus quercuscalicis* was found as far north as Dunkeld, Perthshire (Grid ref. NO 304742). Range expansion by *A. quercuscalicis* is discussed in detail in Chapter 3. Despite being first recorded in Britain in the same year and county as *A. lignicolus* (West Sussex, Hutchinson, 1974), the distribution of *Andricus corruptrix* remains much more restricted with the most northerly record from Ripon, North Yorkshire (Grid ref. SE 355678). The 4 more recently arrived cynipids are largely restricted to south east England (Figure 2.3), although *Andricus aries* has recently been recorded in Devon, and *A. grossulariae* in Hampshire (Schönrogge, pers. comm.).

2.3.2. Rates of spread of invading cynipids in Britain

The mean linear rate of spread per year (linear distance from first UK record to most distant UK record divided by the number of years in between) for each of the 8 cynipid species is shown in Table 2.2. Due to the limited amount of records for all species at the invasion front (with the exception of *A. aries*), these data are best estimates currently available. Rates of spread vary across species, ranging from 3.3 km/year⁻¹ for *Aphelonyx cerricola* to 24.4 km/year⁻¹ (8 times the rate of spread recorded for *A. cerricola*) for *A. lignicolus*, which is widespread throughout most of Britain.

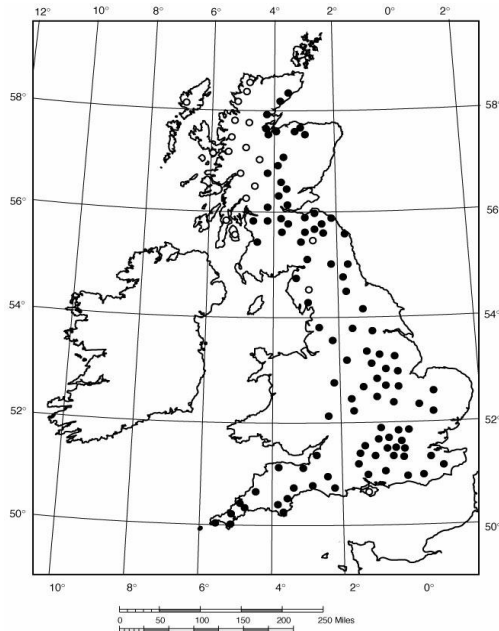
Table 2.2 Mean linear rate of spread (km/year⁻¹) for each of the invading cynipid species across Britain. Since *A. kollari* is already distributed across the entire British mainland, the mean rate for this species is based on the rate of spread from the date of the first record to the date that the most northerly record was collected: *A. aries* (Leach and Shirley, 1999); *A. corruptrix*, *A. lignicolus* (Hutchinson, 1974); *A. grossulariae* (Walker, 2001); *A. kollari* (Smith, 1854); *A. lucidus* (Stone and Sunnucks, 1993); *A. quercuscalicis* (Claridge, 1962); *Aphelonyx cerricola* (Crawley, 1999). All other species are currently expanding their ranges northwards across Britain.

Cynipid Species	Mean linear rate of spread (km/year ⁻¹)
<i>Andricus kollari</i>	9.9
<i>Andricus quercuscalicis</i>	8.0
<i>Andricus lignicolus</i>	24.4
<i>Andricus corruptrix</i>	9.3
<i>Andricus lucidus</i>	4.4
<i>Andricus aries</i>	24.0*
<i>Aphelonyx cerricola</i>	3.3
<i>Andricus grossulariae</i>	22.0

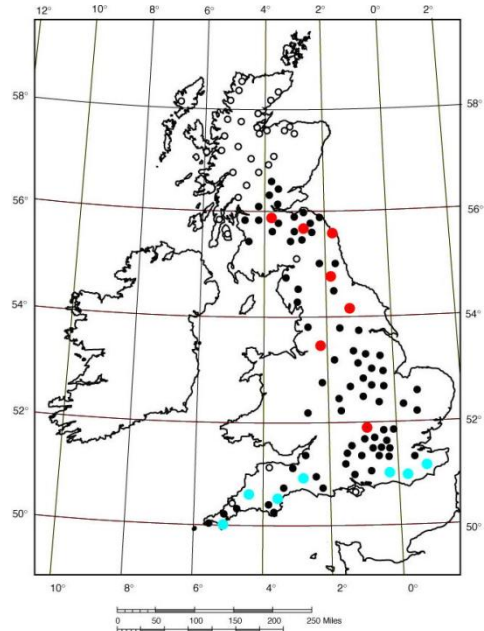
*This value was calculated using regression analysis. See Table 2.3 and Figure 2.4 below for full results.

Figure 2.2 Maps showing the current distributions of invading cynipid species first recorded in Britain prior to 1992. Filled circles indicate each species was present, open circles where absent. Map b) *A. quercuscalicis* also shows east to west transect sites (blue) and north to south transect sites (red) selected for analyses for Chapter 3.

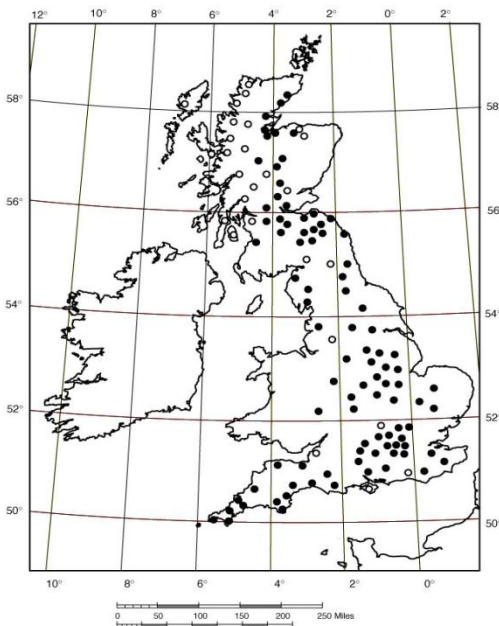
a) *Andricus kollari*



b) *Andricus quercuscalicis*



c) *Andricus lignicolus*



d) *Andricus corruptrix*

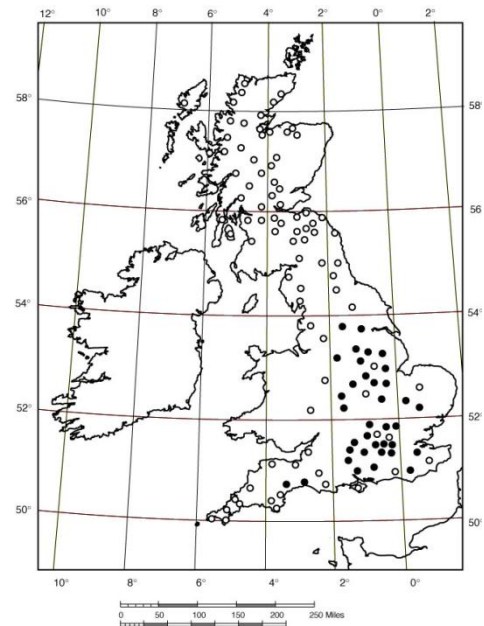
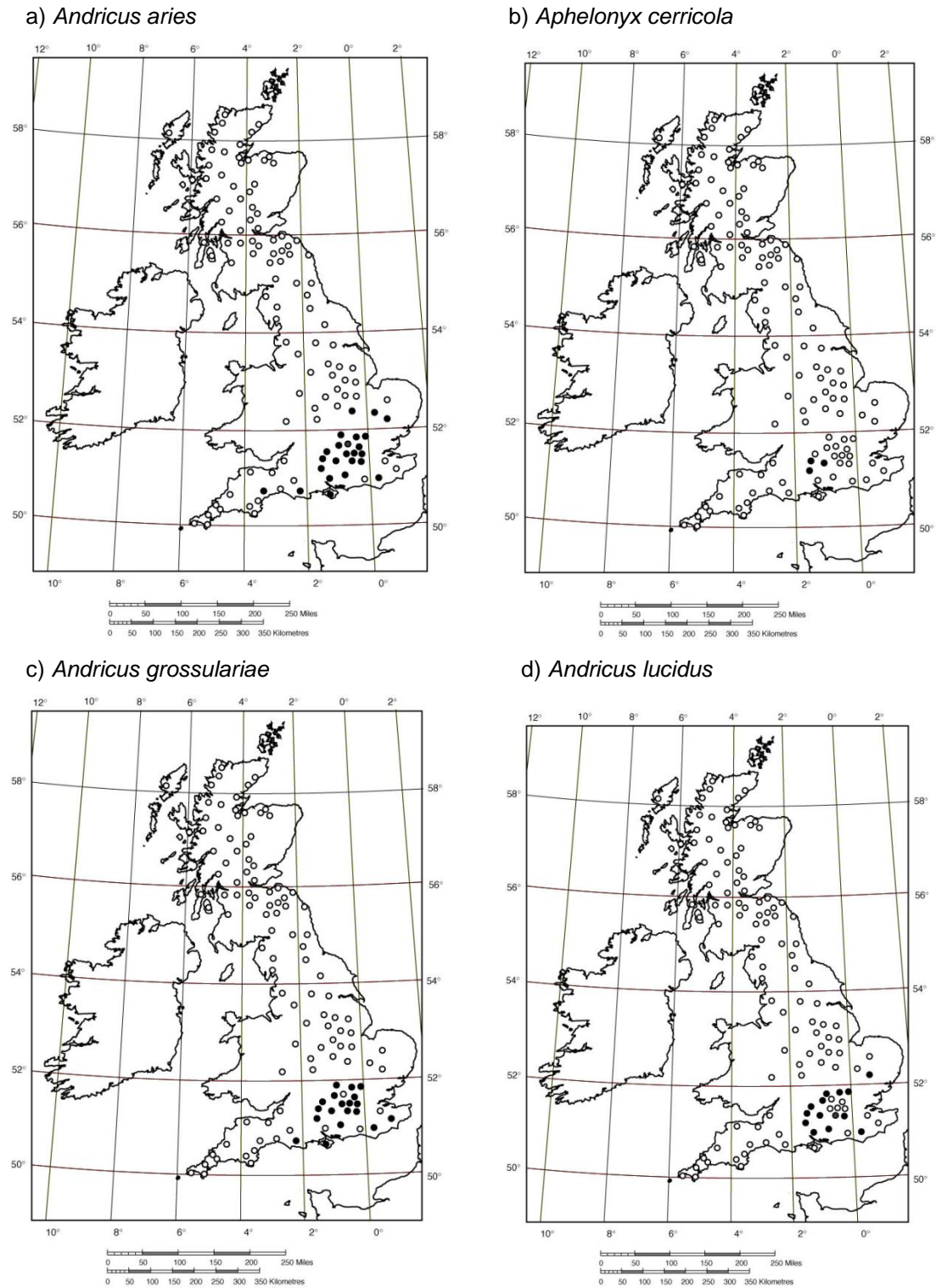


Figure 2.3 Maps showing the current distributions of invading cynipid species first recorded in Britain after 1992. Filled circles indicate each species was present, open circles where absent.

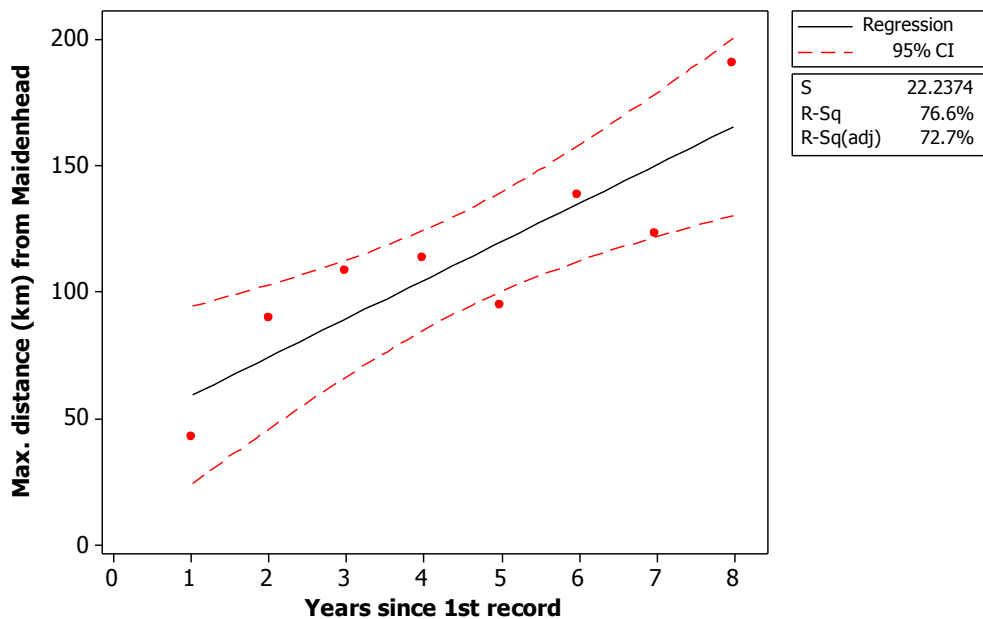


Andricus aries is the only invader in Britain for which sufficient data exists to conduct a regression analysis to examine the pattern and rate of spread at the invasion front of the species since its first record from Maidenhead, Berkshire (1997). The rate of spread for *A. aries* in Britain is linear, occurring at a rate of 24 km per year (Table 2.3, Figure 2.4). Although insufficient to conduct meaningful regression analyses, a small number of additional records are available for some of the new invading species and are listed in the Appendix (see Appendix Table 7.4).

Table 2.3 Summary statistics for the regression analyses for the rate of spread *A. aries*.

Gall Species	Predictor	Coefficient	d.f.	SE Coefficient	F	P
<i>A. aries</i>	Time	24.027	1	1.748	13.75	<0.001

Figure 2.4 The rate of spread of *A. aries* across Britain from the site of first record in Maidenhead, Berkshire.



2.3.3. The communities associated with invading cynipids in Britain

The parasitoid and inquiline assemblages associated with each of the 8 invading cynipid species in Britain are shown in Tables 2.4, 2.5 and 2.6. Records include those from previous studies as well as data collected from rearings in the course of this study. More species were reared from *A. grossulariae* sexual galls (Table 2.4, 16 species) than from all other sexual generation galls. *Andricus grossulariae* is also the only sexual gall of the 4 invaders that arrived in Britain after 1992 to yield any parasitoids or inquilines during this study. These 16 species represent the first records of any parasitoid or inquiline emergence from *A. grossulariae* sexual galls in Britain. Of the first 4 invading gallwasps, new parasitoid species were recorded only from the sexual galls *A. quercuscalicis* (3 species, *C. fungosa*, *M. sericeus*, *O. vernalis*). No parasitoid or inquiline species new to Britain were recorded.

Of the asexual generation galls, *A. kollari* yielded the most parasitoid and inquiline species (Table 2.5, 24 species), almost three times more than *A. lignicolus*, which has the lowest assemblage species richness (9 species) of the 4 cynipids recorded in Britain prior to 1992. The only new parasitoids or inquiline species reared from the asexual generations of the first 4 invading cynipid species during this study were the inquiline *Synergus pallipes* (from the asexual galls of *A. quercuscalicis*) and a single specimen of the inquiline *Ceroptres clavicornis* (from an asexual *A. kollari* gall). Rearings of the 4 invading cynipid species recorded in Britain after 1992 produced numerous new British parasitoid and inquiline records (Table 2.6). Nine species were recorded from asexual *A. lucidus* galls, all of which are the first British records from this gall. A total of 10 species were recorded from *A. aries*, 3 species (*Eurytoma brunniventris*, *Synergus pallidipennis*, *Synergus radiatus/pallipes*) being first records of these species from *A. aries* in Britain. An additional 8 new species were recorded from *A. grossulariae* asexual galls in Britain. Only 2 species have been recorded from *Aphelonyx cerricola* in Britain, one of which (*O. nitidulus*) was reared from the gall for the first time during this study.

Table 2.4 Parasitoid and inquiline species recorded from the sexual galls of invading cynipids in Britain. *Andricus lucidus* is not included because no parasitoid or inquiline species have been recorded from this species in Britain. New British records collected during this study are shown in bold. Sources of other records are indicated by numbers in superscript after the species name in the table: 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 Stone *et al.*, in prep; ⁹ Eady, 1952; ¹⁰ Schönrogge *et al.*, 1995; ¹¹ Schönrogge *et al.*, 1996; ¹² Askew and Neill, 1993; ¹³ Wurzell, 2000; ¹⁴ Jennings, 2001.

Gall Species	<i>Andricus kollari</i>	<i>Andricus quercuscalicis</i>	<i>Andricus lignicolus</i>	<i>Andricus corruptrix</i>	<i>Andricus grossulariae</i>
Parasitoids					
	-	<i>Aprostocetus</i> ³ <i>aethiops</i>	-	-	-
	-	<i>Mesopolobus dubius</i> ³	<i>Mesopolobus dubius</i> ²	<i>Mesopolobus dubius</i> ²	-
	<i>Mesopolobus fuscipes</i> ¹	<i>Mesopolobus fuscipes</i> ⁴	<i>Mesopolobus fuscipes</i> ²	<i>Mesopolobus fuscipes</i> ²	<i>Mesopolobus fuscipes</i>
	<i>Mesopolobus tibialis</i> ²	<i>Mesopolobus tibialis</i> ⁴	<i>Mesopolobus tibialis</i> ²	-	<i>Mesopolobus tibialis</i>
	<i>Mesopolobus xanthocerus</i> ²	<i>Mesopolobus xanthocerus</i> ⁴	<i>Mesopolobus xanthocerus</i> ²	<i>Mesopolobus xanthocerus</i> ²	<i>Mesopolobus xanthocerus</i>
	-	-	-	-	<i>Sycophila flavicollis</i>
	-	-	-	-	<i>Sycophila variegata</i>
	-	-	-	-	<i>Megastigmus dorsalis</i>
	-	-	-	-	<i>Torymus flavipes</i>
	-	<i>Cecidostiba fungosa</i>	-	-	<i>Cecidostiba fungosa</i>
	-	-	-	-	<i>Eupelmus urozonus</i>
	-	-	-	-	<i>Eurytoma brunniventris</i>
	-	-	-	-	<i>Mesopolobus amaenus</i>
	-	-	-	-	<i>Ormyrus nitidulus</i>
	-	-	-	-	<i>Sycophila biguttata</i>
	-	-	-	-	<i>Cecidostiba fungosa</i>
	-	<i>Mesopolobus sericeus</i>	-	-	<i>Mesopolobus sericeus</i>
	-	<i>Ormocerus vernalis</i>	-	-	-
Inquilines					
	-	-	-	-	<i>Synergus gallaepomiformis</i>
Total	3	8	4	3	16

Table 2.5 Parasitoid and inquiline species recorded from the asexual galls of invading cynipids that were present in Britain before 1992. Sources of other records are indicated by numbers in superscript after the species name in the table: 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 Stone *et al.*, in prep; ⁹ Eady, 1952; ¹⁰ Schönrogge *et al.*, 1995; ¹¹ Schönrogge *et al.*, 1996; ¹² Askew and Neill, 1993; ¹³ Wurzell, 2000; ¹⁴ Jennings, 2001.

Gall Species	<i>Andricus kollari</i>	<i>Andricus quercuscalicis</i>	<i>Andricus lignicolus</i>	<i>Andricus corruptrix</i>
Parasitoids				
	<i>Sycophila biguttata</i> ⁵	<i>Sycophila biguttata</i> ¹⁰	-	<i>Sycophila biguttata</i> ²
	<i>Sycophila flavicolis</i> ⁴	-	-	-
	<i>Sycophila variegata</i>	-	-	-
	<i>Eurytoma brunniventris</i> ⁴	<i>Eurytoma brunniventris</i> ¹⁰	<i>Eurytoma brunniventris</i> ⁸	<i>Eurytoma brunniventris</i> ²
	<i>Megastigmus dorsalis</i> ⁶	<i>Megastigmus dorsalis</i> ¹⁰	<i>Megastigmus dorsalis</i> ¹²	<i>Megastigmus dorsalis</i> ⁸
	<i>Megastigmus stigmatizans</i> ⁶	<i>Megastigmus stigmatizans</i> ¹⁰	-	-
	<i>Torymus auratus</i> ⁷	<i>Torymus auratus</i> ¹⁰	<i>Torymus auratus</i> ¹²	-
	-	-	-	<i>Torymus flavipes</i> ²
	<i>Torymus geranii</i> ⁴	<i>Torymus geranii</i> ³	-	-
	-	<i>Ormyrus nitidulus</i> ¹⁰	-	-
	-	-	-	<i>Ormyrus pomaceus</i> ²
	<i>Caenacis lauta</i> ⁴	-	-	-
	<i>Cecidostiba fungosa</i> ²	<i>Cecidostiba fungosa</i> ¹⁰	-	<i>Cecidostiba fungosa</i> ²
	-	<i>Cecidostiba semifascia</i> ¹¹	-	-
	<i>Hobbya stenoata</i> ⁴	-	-	-
	<i>Mesopolobus amaenus</i> ⁴	<i>Mesopolobus amaenus</i> ¹¹	<i>Mesopolobus amaenus</i> ¹²	<i>Mesopolobus amaenus</i> ²
	<i>Mesopolobus fasciventris</i> ⁸	-	-	<i>Mesopolobus fasciventris</i> ²
	<i>Mesopolobus sericeus</i> ⁸	<i>Mesopolobus sericeus</i> ¹⁰	<i>Mesopolobus sericeus</i> ¹²	<i>Mesopolobus sericeus</i> ²
	<i>Mesopolobus tibialis</i> ²	<i>Mesopolobus tibialis</i> ²	-	-
	<i>Eupelmus annulatus</i> ⁸	-	-	-
	<i>Eupelmus urozonus</i> ⁴	<i>Eupelmus urozonus</i> ¹⁰	<i>Eupelmus urozonus</i> ¹²	<i>Eupelmus urozonus</i> ²
	-	<i>Eupelmus vesicularis</i> ⁸	-	-
	<i>Aulogymnus trilineatus</i> ⁸	-	-	-
Inquilines				
	<i>Ceroptres clavicornis</i>	-	-	-
	<i>Synergus gallaepomiformis</i> ⁴	<i>Synergus gallaepomiformis</i> ²	<i>Synergus gallaepomiformis</i> ²	<i>Synergus gallaepomiformis</i> ²
	-	<i>Synergus pallicornis</i> ³	-	-
	<i>Synergus pallidipennis</i> ⁹	-	-	-
	<i>Synergus pallipes</i> ²	<i>Synergus pallipes</i>	-	-
	-	<i>Synergus radiatus</i> ²	-	-
	<i>Synergus reinhardi</i> ²	-	<i>Synergus reinhardi</i> ²	<i>Synergus reinhardi</i> ²
	<i>Synergus umbraculus</i> ²	<i>Synergus umbraculus</i> ¹⁰	<i>Synergus umbraculus</i> ¹²	-
Total	24	18	9	12

Table 2.6 Parasitoid and inquiline species recorded from the asexual galls of invading cynipids that arrived in Britain after 1992. New British records collected during this study are shown in bold. Sources of other records are indicated by numbers in superscript after the species name in the table: 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 Stone *et al.*, in prep; ⁹ Eady, 1952; ¹⁰ Schönrogge *et al.*, 1995; ¹¹ Schönrogge *et al.*, 1996; ¹² Askew and Neill, 1993; ¹³ Wurzell, 2000; ¹⁴ Jennings, 2001.

Gall Species	<i>Andricus grossulariae</i>	<i>Andricus aries</i>	<i>Andricus lucidus</i>	<i>Aphelonyx cerricola</i>
Parasitoids				
	<i>Sycophila biguttata</i>	<i>Sycophila biguttata</i> ⁸	<i>Sycophila biguttata</i>	-
	-	<i>Sycophila flavicolis</i> ⁸	-	-
	<i>Eurytoma brunniventris</i>	<i>Eurytoma brunniventris</i>	<i>Eurytoma brunniventris</i>	-
	<i>Megastigmus dorsalis</i>	<i>Megastigmus dorsalis</i> ¹³	-	-
	-	-	<i>Torymus auratus</i>	-
	<i>Ormyrus nitidulus</i> ⁸	-	-	<i>Ormyrus nitidulus</i>
	<i>Cesidostiba fungosa</i>	-	<i>Cesidostiba fungosa</i>	-
	<i>Mesopolobus sericeus</i>	-	<i>Mesopolobus sericeus</i>	-
	<i>Mesopolobus xanthocerus</i>	-	<i>Mesopolobus xanthocerus</i>	-
	<i>Eupelmus urozonus</i>	-	<i>Eupelmus urozonus</i>	-
Inquilines				
	-	<i>Ceroptres clavicornis</i> ⁸	<i>Ceroptres clavicornis</i>	-
	-	<i>Synergus gallaepomiformis</i> ⁸	-	-
	-	<i>Synergus pallidipennis</i>	-	-
	-	<i>Synergus radiatus/pallipes</i>	-	-
	-	<i>Synergus reinhardi</i> ¹⁴	-	-
	-	<i>Synergus tibialis</i> ⁸	-	-
	<i>Synergus umbraculus</i>	-	<i>Synergus umbraculus</i>	-
	-	-	-	<i>Synergus variabilis</i> ⁸
Total	9	10	9	2

2.4 Discussion

2.4.1. Distributions and rates of range expansion

All invading cynipid species established in Britain before 1992 have a more widespread distribution than recorded during previous surveys conducted in 1994/5, with the exception of *A. kollari* which was already distributed throughout Britain, including the Inner Hebrides, by the 1940's (Wormell, 1982; Walker *et al.*, 2002). This fulfils the prediction that other invading species will continue to expand their ranges across Britain over time. *Andricus lignicolus* is now almost as widespread as *A. kollari* and is found in Sutherland in north east Scotland where it was first recorded in 1996 (Entwhistle, 1996). However, this species has yet to spread to the north west of Scotland or the Outer Hebrides, areas where *Q. cerris* is sparsely distributed. If dispersal is affected by host tree density, it can be predicted that the spread in north west Scotland would be slow relative to areas of high host tree abundance. *Andricus corruptrix* is still expanding its range across Britain. In 1996, *A. corruptrix* was recorded at Frome in Somerset (Walker *et al.*, 2002) and it has since expanded its range further west and was recorded in Bovey Tracey, Devon (Grid ref. SX 816797) during this study. The species has also expanded northwards. In 1994, *A. corruptrix* was found in south Yorkshire and Lincolnshire (Shirley, 1998; Walker *et al.*, 2002) and in this study, asexual generation galls were located as far north as Ripon in North Yorkshire.

This is the first extensive UK survey of the distributions of the more recently invading cynipids (post-1992: *A. aries*, *A. lucidus*, *A. grossulariae*, *Aphelonyx cerricola*). All currently show a much more restricted distribution relative to the first 4 invading cynipids and all 4 species are largely restricted to south east England. This is unsurprising given the relatively short length of time since these species were first recorded in Britain and this study can be considered to be a snapshot showing the current distributions. *Aphelonyx cerricola* is particularly rare and has a very localised distribution within Berkshire, reflected in the low mean linear rate of spread per year. Additionally, all these invading cynipid species have arrived in south east

England, the exception being a single record of the sexual generation of *A. lucidus* (*A. aestivalis*) in Scotland (Cameron, 1893).

Several factors could contribute to observed variation in the rate of dispersal of invading cynipids, particularly the distribution of host oaks (*Q. cerris*, *Q. petraea*, *Q. robur*). The rapid spread of *A. lignicolus*, which reached central Scotland within 15 years of its arrival in Britain (Walker *et al.*, 2002), may be explained in part by unintentional human transport via commercial horticulture. In contrast, the first *A. lignicolus* to reach southern England may have arrived without direct human assistance (Hayward and Stone, 2006). An extensive oak planting programme in Perthshire in the 1980's included trees from southern England, Holland and north west Germany (Walker *et al.*, 2002). The high densities of *A. lignicolus* asexual galls found in this area in 1992 (Walker *et al.*, 2002) suggest that the imported trees carried *A. lignicolus* galls.

The age of available host trees also has an impact on the rate of dispersal on invading cynipids. The sexual generations of both *A. lignicolus* and *A. kollari* can oviposit on even the youngest host trees (Schönrogge, unpubl.). Further spread of *A. lignicolus* into Sutherland in north east Scotland may therefore have been facilitated by extensive planting of *Q. robur* saplings (Walker *et al.*, 2002). Planting cannot by itself be taken as evidence for likely introduction, because increasing use is being made of local seed, notably at Dunrobin Estate, Golspie, Sutherland (Walker *et al.*, 2002). *Andricus kollari* asexual galls are also abundant on young trees at Dunrobin.

Andricus quercuscalicis has a much lower rate of spread than *A. lignicolus* (24.2 km/year for *A. lignicolus* compared with 8 km/year for *A. quercuscalicis*). If we take the rate of spread of *A. lignicolus* at face value, then the lower rate of dispersal in *A. quercuscalicis* may be due to lower availability of host trees of a necessary age for gall induction. *Andricus quercuscalicis* induces galls on the catkins of *Q. cerris* and the acorns of *Q. robur* and thus requires mature trees in both generations of its lifecycle (while *A. lignicolus* require buds in both generations, and so can exploit young trees in each). *Andricus quercuscalicis* is also more host specific than *A.*

lignicolus: asexual generation galls of *A. quercuscalicis* on *Q. petraea* are extremely rare, while *A. lignicolus* galls develop on *Q. robur* and *Q. petraea* equally. The density of suitable hosts must therefore be higher for *A. lignicolus* than *A. quercuscalicis*, which might be reflected in the dispersal rates.

This comparison raises the question of why dispersal rates for *A. kollari* and *A. lignicolus* are so different (9.9 versus 24.4 km/year). Both species have the same oak associations, and, since both are gall buds in both generations, have the same ability to gall both young and mature trees. However, *A. kollari* expanded its range across Britain in the mid-nineteenth century, more than a century before *A. lignicolus*. At that time, oak forests had been substantially depleted due to shipbuilding and charcoal manufacture for iron smelting associated with the Napoleonic wars (reducing availability of hosts for the sexual generations), and *Q. cerris* was less abundant than it is now. It is plausible that *A. kollari* also experienced lower density of appropriate gall induction sites than *A. lignicolus*, resulting in lower range expansion rates. This hypothesis predicts that other recently arriving invaders with the same host requirements as *A. lignicolus* should also show higher range expansion rates than the earlier invaders, and for *A. aries* (20 km/year) and *A. grossulariae* (22 km/year), this is indeed the case. However, range expansion by 2 other host alternators, *A. corruptrix* (9.3 km/year) and *A. lucidus* (4.4 km/year) is substantially slower, so support for this hypothesis is inconsistent.

Rates of spread data presented are the best currently available, with only *A. aries* providing sufficient records for more complete analyses. Should adequate data become available for other species, regression analyses could be used to examine and compare rates of spread, as has been possible for *A. aries*. It could be predicted that as the invasion front moves northwards, invading species will have a continuous and linear rate of spread as shown by *A. aries*, but may slow and level off as species reach northern Scotland. The rate of spread may be slowed in northern Scotland because *Q. cerris* occurs at a lower density than the rest of Britain and is more patchily distributed.

Of the four invading cynipids recorded prior to 1992, *A. corruptrix* has the slowest rate of spread across Britain despite being able to exploit any host oak age class in both generations (Walker *et al.*, 2002). Previous British records together with quantified collections made in this study suggest this species is rarer than the more widespread *A. lignicolus*, *A. kollari* and *A. quercuscalicis* and is distributed thinly and patchily throughout its current range in Britain (Hutchinson, 1974; Walker *et al.*, 2002). Data produced from quantitative webs (see Chapter 4) show that of the 3 invading bud gallers on *Q. cerris* in Britain, *A. corruptrix* is the least abundant. This rarity may explain the slower range expansion of this species. In their native range, *A. lignicolus*, *A. kollari* and *A. quercuscalicis* are generally widespread and abundant (Walker *et al.*, 2002), while *A. corruptrix* is often very local and is rarely abundant (Csóka, pers comm.). This relative rarity could be due to many factors, including unknown specific requirements of host oaks for gall induction, lower fecundity or higher mortality than other more widespread invaders. Laboratory dissections of asexual generation females suggest that potential fecundity is lower in *A. corruptrix* than either *A. lignicolus* or *A. kollari* (Walker *et al.*, 2002).

The 4 most recently invading species (post-1992: *A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*) are much more restricted in their distribution. However, these species show varying rates of spread. *Andricus aries* and *A. grossulariae* are spreading rapidly (Wurzell, 2000; Walker *et al.*, 2002) (Figure 2.3) at a rate comparable with *A. lignicolus* whereas *A. lucidus* and *Aphelonyx cerricola* are still restricted and were only found relatively close to areas where these species were first recorded in Britain. Very little information is available about the distribution and abundance of these 4 species in their native range or the invaded range across continental Europe and most information is anecdotal (Csóka pers. comm.). In its native range, *A. lucidus* is rarely abundant in either generation. *Andricus grossulariae* has a patchy distribution with large inter-tree variation in abundance. *Aphelonyx cerricola* are more commonly found on young trees in areas of woodland where *Q. cerris* has been established for sometime (Csóka pers. comm.), a habitat that is uncommon in Britain and may explain the very restricted distribution of this species. Low rate of dispersal in *Aphelonyx* could also potentially

be associated with the total dependence of range expansion by this species on the distribution of *Q. cerris*, without the ability to successfully induce galls on intervening patches of *Q. petraea* and *Q. robur*.

2.4.2. Parasitoid and inquiline communities

The parasitoid and inquiline assemblages associated with both generations of the 4 cynipids established in Britain prior to 1992 have remained largely unchanged since the last survey in 1994/5. The only exceptions are three new parasitoid species reared from the sexual galls of *A. quercuscalicis* (*C. fungosa*, *M. sericeus*, *O. vernalis*), the inquilines *Synergus pallipes* reared from the asexual galls of *A. quercuscalicis* and a single specimen of *Ceroptres clavicornis* from an asexual *A. kollari* gall. Hypotheses that may explain the limited recruitment over the last 10 years are discussed in depth in Chapter 3 with specific reference to *A. quercuscalicis* (see Chapter 3 Discussion) and these hypotheses are also valid for *A. lignicolus*, *A. kollari* and *A. corruptrix*.

The parasitoid and inquiline species recorded from the 4 recent invaders (*A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*) represent the first comprehensive baseline data for these species in Britain. Sixteen species were reared from the sexual generation of *A. grossulariae* galls on *Q. cerris*, all of which are native to Britain and some of the parasitoid species are shared with the sexual galls of the other 4 established cynipid species on *Q. cerris* (see Table 2.3). Examples include *Mesopolobus xanthocerus*, *M. fuscipes* and *M. tibialis*, which are also recorded from *A. grossulariae* in the native range (Melika and Abrahamson, 2002). *Andricus grossulariae* shares all 3 species with *A. kollari*, *A. lignicolus* and *A. quercuscalicis* and 2 species with *A. corruptrix* (*Mesopolobus xanthocerus*, *M. fuscipes*). In the native range, 40 species of parasitoids and inquilines have been recorded from *A. grossulariae* sexual galls (Melika and Abrahamson, 2002; Pujade-Villar *et al.*, 2003). In addition to the 16 species already recorded, another 6 are regularly recorded from the parasitoid and inquiline pool in Britain. It can therefore be predicted that the species richness of the assemblage associated with *A. grossulariae* should increase with the residence time of the gall in Britain (Schönrogge *et al.*, 1998). This

prediction can also be made for the sexual generation of *A. lucidus*. To date, no parasitoids or inquilines have been reared from the sexual generation gall of this species in Britain, largely due to the current rarity of this sexual generation gall in Britain. Fourteen species of parasitoids and inquilines have been reared from this gall in the native range (Melika and Abrahamson, 2002), ten of which are commonly recorded from the parasitoid and inquiline pool in Britain.

Patterns of recruitment in the asexual generations of the 4 invading cynipids recorded after 1992 are similar to those observed in the sexual generations. Potential future parasitoid and inquiline recruitment is particularly high for *A. grossulariae* and *Aphelonyx cerricola*. Currently 9 species have been reared from asexual galls of *A. grossulariae* in Britain. In the native range, 40 species have been recorded (Pujade-Villar *et al.*, 2003), of which another 18 parasitoid and inquiline species are native to Britain. Only 2 species have been recorded from *Aphelonyx cerricola* in Britain to date, while 38 species have been recorded from this species in its native range (Melika and Abrahamson, 2002), 14 of which are also native to Britain.

Although the discussion above has alluded to the hypothesis that recruited parasitoids and inquilines are from the native community (native recruitment hypothesis), an alternative non-exclusive hypothesis is that the parasitoid species attacking the host in its invaded range are lineages that have pursued the host from the native range, and so themselves represent invading genotypes (pursuit hypothesis) (Hayward and Stone, 2005). These alternatives can potentially be discriminated with population genetic methods.

Although this study provides the first baseline data about the distribution and parasitoid assemblages of the 4 more recently invading cynipids (*A. aries*, *A. grossulariae*, *A. lucidus*, *Aphelonyx cerricola*), some comparisons can be made with the invasion history of *A. quercuscalicis*, the most comprehensively studied invading cynipid in Britain. Similar to *A. quercuscalicis*, these species have a restricted distribution at this early stage of their invasion in Britain, mainly being recorded in south east England. However, parasitoid and inquiline recruitment has been much

more rapid in the 4 species than reported for *A. quercuscalicis*, particularly for *A. grossulariae*. *Andricus grossulariae* was first recorded in Greater London in 2001. Only four years later, 16 species of parasitoids and inquilines had been reared from the sexual generation and 9 from the asexual generation whereas it was 25 years after the first recorded asexual *A. quercuscalicis* galls that any parasitoids were reared from the gall (Hails *et al.*, 1990).

While it can be predicted that the distribution of these species will continue to change in the future as they expand their ranges north and west across Britain as the established invading cynipids have, the way in which the communities associated with these 4 species develop over time is more difficult to predict. It could be argued that due to the presence of *A. quercuscalicis*, some parasitoid species have adapted to find hosts on the acorns on *Q. robur*. If so, the parasitoid and inquiline assemblages associated with *A. lucidus* and *A. grossulariae* asexual galls would be expected to be similar to that of *A. quercuscalicis*. 65% of parasitoid and inquiline species are shared between *A. lucidus* and *A. quercuscalicis* asexual galls and 60% of parasitoid and inquiline species are shared between *A. grossulariae* and *A. quercuscalicis* asexual galls. Stronger support for the general hypothesis that parasitoids are shared with galls on the same part of the same host at the same time of year comes from the overlap observed in the parasitoid assemblages currently associated with sexual *A. grossulariae* and *A. quercuscalicis* galls, both found on catkins of *Q. cerris*: Five of the 8 parasitoid species that attack the sexual galls of *A. quercuscalicis* in Britain also attack the sexual galls of *A. grossulariae*. Continued monitoring of these cynipid communities will determine if recruitment differs from established invading species or follows a similar but accelerated pattern to that observed in *A. quercuscalicis*.

Chapter 3

Spatial and temporal changes in the dynamics of *Andricus quercuscalicis* and its associated communities in Britain

3.1 Introduction

There is considerable interest in the study of invading species and the development of communities of natural enemies associated with them. Long-term studies of invading species and their natural enemies are particularly valuable because they allow the study of changes in community dynamics in both time and space. Moving along the invasion route away from the native range, ever more recently invaded communities are encountered and a spatial series thus equates to a time series along the invasion route. Such invasions are large-scale natural experiments (Elton, 1958; Diamond, 1986; Cornell and Hawkins, 1993) that can be used to test theories concerning dynamic changes within communities (Pimm, 1982; Pimm *et al.*, 1991; De Angelis, 1992). Studies of invasions also have an obvious applied value when the invading organism is a pest species (Otake *et al.*, 1984; Greathead, 1989; Moriya *et al.*, 1989; Stone *et al.*, 1995; Willis and Memmott, 2005; Grapputo *et al.*, 2005; Aebi *et al.*, 2007). Such studies may also be relevant for monitoring potential future climatic change. Current studies on the impact of climate change concentrate on distribution changes of individual species (Crozier, 2003; Parmesan and Yohe, 2003; Hitch and Leberg, 2007) but to my knowledge there are none that look at the community context that the species

is in. Looking at developing communities following the range expansion of cynipid hosts could potentially provide predictions about community changes following range expansion as a consequence of climatic change.

Several cynipids of the genus *Andricus* provide examples of well-documented natural invasions across Europe (Askew, 1984; Stone and Sunnucks, 1993; Schönrogge *et al.*, 1994; 1995; 1996; Walker *et al.*, 2002). The invasion of the knopper gallwasp, *Andricus quercuscalicis* has been particularly well documented since its arrival in Britain in the late 1950's (Claridge, 1962; Hails and Crawley, 1991; Schönrogge *et al.*, 1994; 1995; 1996). The invasion history of this species is described fully in Chapter 1 (Section 1.5).

Previous studies of the development of the parasitoid community associated with knopper galls in Britain (Collins *et al.*, 1983; Hails *et al.*, 1990; Schönrogge *et al.*, 1994; 1995; 1996; Stone *et al.*, 1995) show that the communities in the invaded range of *A. quercuscalicis* have undergone considerable change over time in both species abundance and richness. This can be considered to have occurred in two phases: 1) Following an initial rapid increase in species richness during the 1980's (Hails *et al.*, 1990), substantial species turnover resulted in changes in species composition (Schönrogge *et al.*, 1994; 1995; 1996). This turnover resulted in an increasing similarity between British and continental parasitoid communities attacking knopper galls (Stone and Sunnucks, 1993; Schönrogge *et al.*, 1996). 2) A pronounced change in the abundance of inquilines (from zero to an average of more than one inquiline per gall) occurred in the early 1990s' in south eastern England (Schönrogge *et al.*, 1996). Subsequently, parasitoid attacks on inquilines in knopper galls increased in range and abundance.

Following changes within the communities in the invaded range, Schönrogge *et al.* (1996) predicted that should the region of high inquiline abundance spread north and west across Britain, following the range expansion by *A. quercuscalicis*, the pattern of increased parasitoid species richness would follow. The authors also suggested that the parasitoid community in the invaded range would (i) continue to converge (in terms of

species composition) on that of the native range and (ii) continue to increase in species richness with increasing residence time of *A. quercuscalicis* in Britain. This would be consistent with a large comparative study (Cornell and Hawkins, 1993) investigating the effect of residence time on parasitoid recruitment (though the relationship was not consistent across invading species).

Here, I describe changes in distribution and species composition that have occurred in the community associated with knopper galls over the last 15 years in different parts of Britain following continued range expansion of this species to the north and west. My results are compared with studies of the same community in the native and invaded range of *A. quercuscalicis* in continental Europe and earlier studies in Britain (Hails *et al.*, 1990; Stone *et al.*, 1995; Schönrogge *et al.*, 1995). More specifically, I will explore geographical trends by comparing species abundance and richness from north/south and east/west transects across Britain.

I will test the following predictions: (1) That the high inquiline abundance recorded from knopper galls in south England will spread north across Britain with *A. quercuscalicis* range expansion, resulting in a wider distribution of parasitoids attacking knopper galls across Britain (2) That inquiline/parasitoid abundance and diversity will be higher to the east and south of Britain where this gallwasp is longer established (3) That the parasitoid community of the asexual galls in the invaded range is continuing to converge on that of the native range with increasing residence time of *A. quercuscalicis* in Britain.

3.2 Methods

3.2.1. Collection, rearing and identification of knopper galls and their associated communities

In a country-wide survey of asexual *A. quercuscalicis* galls, the current distribution of the host, associated inquilines and parasitoids were determined across Britain for comparison with the last detailed survey of 1991/2 (Schönrogge *et al.*, 1995; 1996). Over 100 sites (see Appendix, Table 7.1) where both *Quercus robur* and *Q. cerris* were present were searched for asexual galls of *A. quercuscalicis*. During this survey, a sample of 150 *A. quercuscalicis* asexual knopper galls were collected from 14 sites across each of 2 transects: a north to south transect from Falkirk, central Scotland to Knebworth, Hertfordshire (7 sites) and an east to west transect across southern England from Ashford, Kent to Porthleven, Cornwall (7 sites). Table 3.1 provides the locations of each of the sites selected for both transects (also see map in Chapter 2, Figure 2.2). I aimed to collect 150 knopper galls from each site, with a total of 2100 galls reared individually. A sample size of 150 galls is sufficient to rear most of the parasitoid assemblage associated with any given gall type (McArdle, 1990; Schönrogge, 1994). Additionally, in order to map the current limit of inquiline infestation of knopper galls in Britain, galls were collected and reared from 16 sites in central Scotland (Perthshire, Fife, Strathclyde and Lothian) (see Figure 3.2). Sample sizes were variable (see Table 3.2), constrained by the rarity of galls at many of the sites.

Each gall was dissected, separating the inner gall (chamber which contains the gall-former) from the outer gall, to allow for differentiation between those parasitoids attacking the gall-former and those attacking inquilines inhabiting the outer walls of the knopper galls (Schönrogge *et al.*, 1996).

Table 3.1 Locations of the 7 sites along each of the 2 transects selected north/south and east/west across Britain. Northings and eastings are also given as these were used in analyses of geographical trends.

Site	Grid Reference	Northing	Easting
North to south transect			
Falkirk, Stirlingshire	NS 905786	6793	2894
Kelso, Roxburghshire	NT 708348	6341	3711
Alnwick, Cumbria	NU 173135	6146	4169
Gilsland, Northumberland	NY 607692	5700	3645
Ripon, North Yorkshire	SE 347672	4678	4349
Tatton, Cheshire	SJ 752813	3814	3751
Knebworth, Hertfordshire	TL 226213	2209	5223
East to west transect			
Porthleven, Cornwall	SW 626268	2545	1628
Bodmin, Cornwall	SX 074667	7060	2040
Dawlish, Devon	SX963767	7798	2967
Yeovil, Somerset	ST 597168	1170	3602
Horsham, West Sussex	TQ 198312	1317	5199
Scotney, Kent	TQ 692359	1351	5686
Ashford, Kent	TR 000441	1456	5970

Table 3.2 Locations of sites in central Scotland which are at the current limit of inquiline infestation of knopper galls in Britain showing the number of galls reared from each site.

Location	Grid reference	<i>n</i>
South Queensferry, Midlothian	NT 087788	150
Holyrood, Edinburgh	NT 274737	42
Grange, Edinburgh	NT 233712	23
Rosyth, Fife	NT 105839	12
Kincardine, Fife	NS 952876	16
Falkland, Fife	NO 251075	24
Eskine, Strathclyde	NS 453738	150
Kelvinside, Glasgow	NS 561675	84
Pollock Country Park, Glasgow	NS 562622	115
Falkirk, Central Region	NS 905786	150
Muiravonside, Central Region	NS 958763	56
Linlithgow, West Lothian	NT 037785	150
Torphichen, West Lothian	NS 974722	82
Bathgate, West Lothian	NS 956700	22
Birnam, Perthshire	NO 954706	9
Dunkeld, Perthshire	NO 304742	4
Total galls reared		1239

All rearings were stored in an outside insectary and emerging adult gallwasps, inquilines and parasitoids were collected weekly, preserved in alcohol and identified using appropriate keys (Askew and Thúroczy, in prep.; Pujade-Villar *et al.*, in prep.). Identification of voucher specimens were confirmed by expert taxonomists of parasitoids (Dr. R. R. Askew, UK) and cynipid inquilines (Dr. G. Melika, The Plant Protection and Soil Conservation Service of County Vas, Hungary).

3.2.2. Data

From the rearing results, the following parameters about the inquilines in the outer gall and their associated parasitoid assemblages were extracted:

1. parasitoid abundance = parasitoids emerged from the outer gall
2. inquiline abundance = inquilines emerged from the outer gall + parasitoid abundance
3. inquiline survival = inquiline abundance - parasitoid abundance
4. parasitoid attack rate = parasitoid abundance/inquiline abundance*
5. parasitoid species richness = number of parasitoid species per gall

*The number of hosts available varies in the outer gall depending on the number of inquilines in each gall but is always one for the inner gall which contains only the gall-former as a potential resource for attacking parasitoids.

For inner cell parasitoids, host availability is taken as the sample size. For parasitoids that only attack inquilines, mean attack rates were calculated only over outer wall samples that contained inquiline hosts. These were identified by virtue of their yielding either inquilines or parasitoids. Parasitoids emerging from the outer walls of galls could have attacked either an inquiline or another parasitoid (Askew, 1961). However, Schönrogge *et al.* (1995) showed during dissections of 3800 asexual galls of *A. quercuscalicis* that hyper-parasitism in these galls is virtually absent and it is therefore

assumed all outer wall parasitoids attacked inquiline hosts. Inquilines are not analysed by species as almost all inquilines recorded were *S. gallaepomiformis* with sample sizes of all other species being too small for separate analyses.

3.2.3. Statistical Modelling

Using generalized linear models, all the parameters mentioned under 3.2.2. were analysed for geographical trends. Northerliness and easterliness were fitted as UK grid references and their squared terms were included to potentially identify non-linear geographic trends. Data from the north - south and east - west transect were analysed in turn.

Model terms were tested for significance on deletion and the model simplified until all retained terms were significant (minimum adequate model; Crawley, 2004). All models were inspected for overdispersion (models with binomial errors) and checked for heteroscedasticity and the normality of errors (Crawley, 2004). GLM analyses were carried out using S-plus (Insightful Corp., 2005).

Specifically, inquiline and parasitoid abundance data were analysed using $\log(x+1)$ transformed response variables, normal errors and an identity link function. To control for inquiline abundance, i.e. resource availability, for parasitoids emerging from the outer wall, this parameter was fitted as an explanatory variable in the parasitoid abundance models before assessing the geographical variables.

Multiple parasitism of the gall-former was never observed and the response is therefore binary (present/absent). Parasitoid attacks on the gall-former were analysed using binomial errors and a logit link function as was the proportions of inquiline survivors.

We expect parasitoid species richness to be affected by sampling effort, i.e. inquiline abundance. As for parasitoid abundance models, inquiline abundance was thus fitted as an explanatory variable before assessing the significance of the geographical variables.

3.3 Results

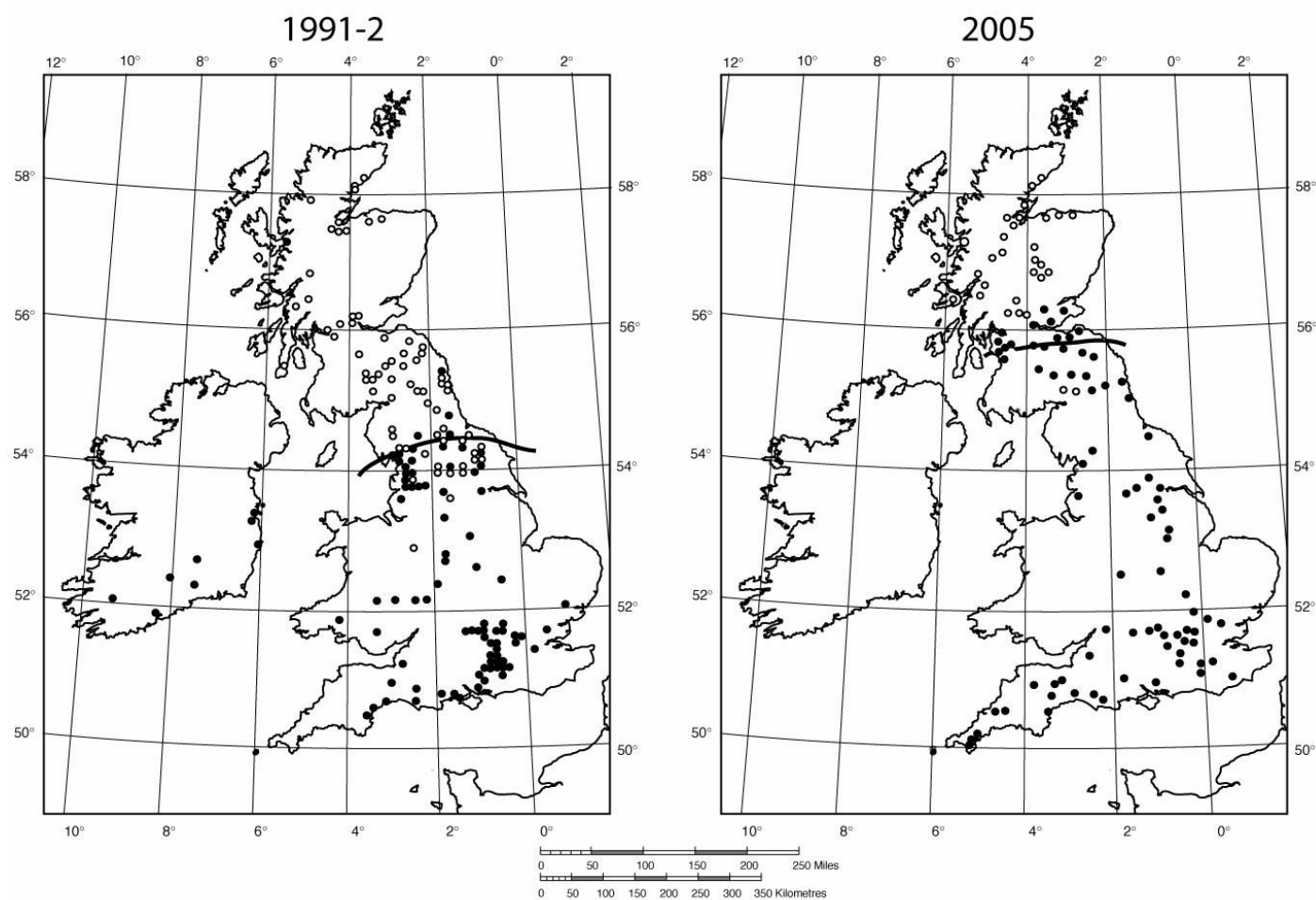
3.3.1. The current distribution of *A. quercuscalicis* across Britain

The survey conducted as part of this study shows that there has been significant northwards range expansion of *A. quercuscalicis* of approximately 122 km since the 1991/2 survey, spreading at an average linear rate of 8 km yr⁻¹. Figure 3.1 shows the distribution of *A. quercuscalicis* in Britain, comparing the 1991/2 and its current distribution. The most northerly record for *A. quercuscalicis* found during this survey was Dunkeld, Perthshire, although this species is sporadic and rare north of the central belt of Scotland.

3.3.2. The current distribution of *Synergus* inquiline infestation of knopper galls across Britain

There has been significant northwards range expansion of *Synergus gallaepomiformis* of approximately 280 km since the last survey in 1991/92, over twice the distance that their host *A. quercuscalicis* has moved north during the same 15 year period. High infestation rates (as defined by Schönrogge *et al.*, 1996, ≥ 1 inquiline per gall) were found as far north as Ripon in North Yorkshire (Mean: 6.34 inquilines per gall). Infestation rates decreased north of this site and were low (<1 inquiline per gall), the lowest being a mean infestation of 0.05 inquilines per gall at Falkirk.

Figure 3.1 The changing distribution of *A. quercuscalicis* and its inquiline over the last 15 years. Black circles: sites where *A. quercuscalicis* asexual galls were recorded. Open circles: sites surveyed but galls absent. The black line represents the northern limit of inquiline attack.



3.3.3. Community composition of *A. quercuscalicis* asexual galls across Britain

The parasitoid and inquiline species emerging from 2100 galls collected from the fourteen sites are listed in Table 3.3, which also shows the number of sites where each species was present. Three inquiline *Synergus* cynipids were reared from asexual generation galls, of which *S. gallaepomiformis* was the most common, while *S. umbraculus* and *S. pallipes* were comparatively rare. This is the first record of *Synergus pallipes* from asexual generation *A. quercuscalicis* galls in Britain. *Synergus pallipes* was recorded at two sites (Ashford and Knebworth) in south east England.

Table 3.3 Parasitoid and inquiline species emerging from 14 sites from north/south and east/west transects across Britain. I – specimens reared from the inner gall. O – specimens reared from the outer gall. Where species emerged from the inner gall and outer gall, the number of individuals that emerged from each part is given in parentheses. The last two columns show the number of sites where each species was present along both transects.

Family	Genus	Species	Inner Cell (I)/Outer Cell(O)	No. of 7 sites (north to south)	No. of 7 sites (east to west)
Pteromalidae	<i>Mesopolobus</i>	<i>amaenus</i>	I	1	1
		<i>sericeus</i>	I(4)/O (414)	6	5
		<i>Cecidostiba fungosa</i>	O	5	6
Eurytomidae	<i>Eurytoma</i>	<i>brunniventris</i>	O	3	3
	<i>Sycophila</i>	<i>biguttata</i>	I (1)/(1)	1	0
Torymidae	<i>Torymus</i>	<i>auratus</i>	O	2	1
	<i>Megastigmus</i>	<i>dorsalis</i>	I	0	1
		<i>stigmatizans</i>	I	0	1
Eupelmidae	<i>Eupelmus</i>	<i>urozonus</i>	O	3	2
Ormyridae	<i>Ormyrus</i>	<i>nitidulus</i>	I	1	1
Cynipidae	<i>Synergus</i>	<i>gallaepomiformis</i>	O	7	7
		<i>umbraculus</i>	O	3	0
		<i>pallipes</i>	O	1	1

Nine parasitoid species emerged from knopper galls reared from sites across both transects. Six species attacked the gall-former in the inner gall (*Mesopolobus sericeus*, *Mesopolobus amaenus*, *Ormyrus nitidulus*, *Sycophila biguttata*, *Megastigmus stigmatizans*, *Megastigmus dorsalis*), while 6 species attacked inquiline hosts in the outer gall (*Mesopolobus sericeus*, *Torymus auratus*, *Cecidostiba fungosa*, *Eurytoma brunniventris*, *Sycophila biguttata* and *Eupelmus urozonus*) (Table 3.3). *Mesopolobus sericeus* and *S. biguttata* emerged from both the inner and outer gall. *Mesopolobus sericeus* (11/14 sites over both transects) and *C. fungosa* (11/14 sites) were the most widespread parasitoids. At two sites, Alnwick and Porthleven, no parasitoids were reared.

The inquiline *S. gallaepomiformis* was widespread and was found at all sites. *Synergus umbraculus* showed a more localized distribution and was restricted to south east England as was *S. pallipes* which was recorded only at Knebworth and Ashford. Geographical patterns in community composition are discussed in section 3.3.6. below.

3.3.4. Parasitoid and inquiline abundance and attack rates

Of 2100 galls collected from the 14 sites along both transects, 61% produced no inquilines or parasitoids. However, at least one specimen emerged at each of the 14 sites although at some sites, notably those to the extreme west and north, attack rates were lower. Parasitoid attack rates of the gall-former within the inner chamber of the gall are considered separately (see section 3.3.5.).

North to south transect

Table 3.4 shows the abundances and survival rates for galls at each site along the north to south transect. Mean inquiline abundances per gall were lowest at Falkirk (Mean \pm S.E.: 0.054 \pm 0.021), the most northerly site, followed by Alnwick (0.074 \pm 0.038), where no parasitoids were reared. At both these sites *S. gallaepomiformis* was the only

inquiline species to emerge. The most common outer gall parasitoid was *M. sericeus*, recorded at all sites except Alnwick, followed by *C. fungosa*, which emerged from all sites except Alnwick and Falkirk. The highest attack rates were recorded for *C. fungosa* (3.867 ± 0.327). Attack rates were higher at the 3 sites at the southern end of the transect (Knebworth, Tatton and Ripon). Tatton had the highest parasitoid attack rate closely followed by Ripon (Tatton 5.368 ± 0.409 , Ripon 4.666 ± 0.336). Tatton also had the highest inquiline survival and the highest total parasitoid and inquiline abundance (16.140 ± 1.060).

East to west transect

Table 3.5 shows the abundances and survival rates for galls at each site along the east to west transect. Mean overall parasitoid and inquiline abundance were lowest at Porthleven in Cornwall (0.054 ± 0.034), the most westerly site. Only 2 inquilines, both *S. gallaepomiformis*, emerged from the outer gall. The most common outer wall parasitoid was *C. fungosa*, which was recorded at all sites except Porthleven. Abundance for this parasitoid were highest at Yeovil (4.759 ± 0.330), this site also having the highest overall parasitoid and inquiline abundance (4.792 ± 0.338), closely followed by Ashford (4.332 ± 0.432), the most easterly site.

With reference to previous studies, the maximum and average abundance per gall for all parasitoid species are summarised in Table 3.6.

Table 3.4 Mean parasitoid (outer wall only) and inquiline abundance (\pm SE) (north to south transect).

SITE	FALKIRK	KELSO	ALNWICK	GILSLAND	RIPON	TATTON	KNEBWORTH
SPECIES							
<i>Cecidostiba fungosa</i>	0	0.120 \pm 0.028	0	0.047 \pm 0.021	3.800 \pm 0.393	3.867 \pm 0.327	2.278 \pm 0.258
<i>Mesopolobus sericeus</i>	0.007 \pm 0.007	0.200 \pm 0.035	0	0.053 \pm 0.023	0.547 \pm 0.112	1.327 \pm 0.218	0.060 \pm 0.032
<i>Mesopolobus amaenus</i>	0	0.007 \pm 0.007	0	0	0	0	0
<i>Eurytoma brunniventris</i>	0	0	0	0	0.133 \pm 0.037	0.027 \pm 0.016	0.113 \pm 0.042
<i>Eupelmus urozonus</i>	0	0	0	0	0.153 \pm 0.042	0.060 \pm 0.029	0.073 \pm 0.021
<i>Torymus auratus</i>	0	0	0	0	0.033 \pm 0.014	0.087 \pm 0.030	0
<i>Ormyrus nitidulus</i>	0	0	0	0	0	0	0.007 \pm 0.007
<i>Sycophila biguttata</i>	0	0	0	0	0	0	0.007 \pm 0.007
Total inquiline (<i>Synergus</i> spp.) abundance	0.054 \pm 0.021	0.614 \pm 0.044	0.074 \pm 0.038	0.240 \pm 0.052	6.343 \pm 0.620	16.140 \pm 1.060	3.344 \pm 0.331
Parasitoid emergence per gall from the outer wall	0.007 \pm 0.007	0.327 \pm 0.042	0	0.100 \pm 0.034	4.666 \pm 0.336	5.368 \pm 0.409	2.536 \pm 0.286
Total parasitoid attack rates of the gall-former	0	0.007 \pm 0.007	0	0	0	0	0.007 \pm 0.007
Total emergence per gall (+gall-former)	0.054 \pm 0.021	0.621 \pm 0.054	0.074 \pm 0.038	0.240 \pm 0.052	6.343 \pm 0.620	16.140 \pm 1.060	3.351 \pm 0.338
Proportion of galls with emergence	0.05	0.30	0.05	0.15	0.67	0.95	0.68

Table 3.5 Mean parasitoid (outer wall only) and inquiline abundance (\pm SE) (east to west transect).

SITE	PORTHLEVEN	BODMIN	DAWLISH	YEOVIL	HORSHAM	SCOTNEY	ASHFORD
SPECIES							
<i>Cecidostiba fungosa</i>	0	0.060 \pm 0.027	0.536 \pm 0.121	3.033 \pm 0.328	0.205 \pm 0.058	0.199 \pm 0.087	2.503 \pm 0.373
<i>Mesopolobus sericeus</i>	0	0.146 \pm 0.046	0.086 \pm 0.047	0.099 \pm 0.050	0.007	0	0.046 \pm 0.020
<i>Mesopolobus amaenus</i>	0	0	0	0.013 \pm 0.009	0	0	0
<i>Eurytoma brunniventris</i>	0	0	0	0.007 \pm 0.007	0	0.007 \pm 0.007	0.080 \pm 0.026
<i>Eupelmus urozonus</i>	0	0	0	0	0	0.007 \pm 0.007	0.007 \pm 0.007
<i>Torymus auratus</i>	0	0	0	0	0	0	0.020 \pm 0.011
<i>Megastigmus stigmatizans</i>	0	0	0.033 \pm 0.015	0	0	0	0
<i>Megastigmus dorsalis</i>	0.007 \pm 0.007	0	0	0	0	0	0
<i>Ormyrus nitidulus</i>	0	0	0.007 \pm 0.007	0	0	0	0
Total inquiline (<i>Synergus</i> spp.) abundance	0.047 \pm 0.033	1.053 \pm 0.124	1.233 \pm 0.187	4.759 \pm 0.330	0.326 \pm 0.068	0.326 \pm 0.094	4.325 \pm 0.427
Parasitoid emergence per gall from the outer wall	0	0.185 \pm 0.055	0.623 \pm 0.149	3.139 \pm 0.345	0.212 \pm 0.059	0.212 \pm 0.087	2.649 \pm 0.368
Total parasitoid attack rates of the gall-former	0.007 \pm 0.007	0.020 \pm 0.011	0.040 \pm 0.159	0.033 \pm 0.015	0	0	0.007
Total emergence per gall (+gall-former)	0.054 \pm 0.034	1.073 \pm 0.129	1.273 \pm 0.192	4.792 \pm 0.338	0.326 \pm 0.068	0.326 \pm 0.094	4.332 \pm 0.432
Proportion of galls with emergence	0.02	0.45	0.3.3	0.87	0.14	0.15	0.68

Table 3.6 The number of specimens emerged per gall based on both the east to west and north to south transects in comparison to rearing results summarised in Schönrogge *et al.*, 1996 and Hails *et al.*, 1990. Parasitoids which attack inquiline hosts can emerge with more than one specimen per gall because each gall can contain multiple hosts. The mean attack rate per gall included only those samples in which the species were present.

Species	Max. abundance (specimens/gall)	Mean abundance (specimens/gall)	<i>n</i> (number of sites where present)	Max. abundance after Schönrogge <i>et al.</i> (1996)	Max abundance after Hails <i>et al.</i> (1990)
<i>M. sericeus</i>	1.330	0.250	10	1.401	0.037
<i>M. amaenus</i>	0.013	0.010	2	0.0133	0.166
<i>C. fungosa</i>	3.800	2.360	11	-*	-
<i>E. brunniventris</i>	0.127	0.062	6	0.360	-
<i>S. biguttata</i>	0.007	0.007	1	0.0501	0.004
<i>T. auratus</i>	0.087	0.047	3	0.0132	-
<i>M. dorsalis</i>	0.007	0.007	1	0.0035	-
<i>M. stigmatizans</i>	0.020	0.020	1	0.0050	-
<i>E. urozonus</i>	0.188	0.063	4	0.101	0.007
<i>O. nitidulus</i>	0.007	0.007	2	0.0261	-

* The first record for *C. fungosa* prior to this study is at Silwood Park, Berkshire, where the abundance was 3.2 (Schönrogge and Crawley, 2000).

The most significant change to previous studies is the spread and abundance of *Cecidostiba fungosa*, which was absent from the parasitoid assemblage in previous studies and is now the most numerous parasitoid with a maximum average abundance of 3.8 specimens per gall at Ripon, North Yorkshire.

3.3.5. Parasitoid attack of the gall-former

North to south transect

Gall-former mortality due to parasitism was low at all sites across both transects (see Tables 3.4 and 3.5). Of 1050 galls reared across the north to south transect, only 7 (0.007%) parasitoids attacked the gall-former. At 3 sites (Alnwick, Gilsland and Ripon), no parasitoids emerged from the inner gall. The highest number of inner gall parasitoids reared was from Kelso (four individuals). This site and Knebworth, the most southerly site, had the highest inner gall parasitoid diversity, with 2 species (*M. sericeus*, *M.*

amaenus) recorded. Only one species (*M. sericeus*) was recorded at Falkirk, the most northerly site. *M. sericeus* was the most common parasitoid of the gall-former across the north to south transect.

East to west transect

The numbers of parasitoids attacking the gall-former were almost 3 times higher on the east to west transect, compared with the north to south. However, attack rates were low with 20 parasitoid individuals emerging from inner galls of 1050 galls reared (2%). Species diversity was the same for the east to west as the north to south transect (4 species) but species composition differed. While *M. sericeus* and *O. nitidulus* were recorded from both transects, *M. amaenus* and *S. biguttata* were recorded only from the north to south transect and *M. dorsalis* and *M. stigmatizans* only from the south. Dawlish had the highest number of inner gall parasitoids (6 individuals) and also the highest inner gall parasitoid diversity with 3 species (*M. stigmatizans*, *O. nitidulus*, *M. sericeus*) recorded, followed by Yeovil with 2 species (*M. sericeus* and *M. dorsalis*). No parasitoids emerged from the inner galls from Horsham. As for the north to south transect, *M. sericeus* was the most common parasitoid of the gall-former.

When compared with Schönrogge *et al.* (1996), the attack rates for *S. biguttata* have declined by one order of magnitude, with only one specimen reared, and similarly, attack rates for *O. nitidulus* have declined by one order of magnitude and only 2 specimens were reared, however, attack rates are higher than those recorded by Hails *et al.* (1990) (see Table 3.6). Some species continue to be rare members of the parasitoid assemblage and were recorded from only one or two sites (*M. dorsalis*, *M. stigmatizans*).

3.3.6. Geographical trends in species abundance and survival across Britain

When testing for trends in geographical locations from east to west and south to north, easterliness was tested only for the east to west transect and northerliness only for the north to south transect.

Inquiline abundance

Inquiline abundance declines with latitude on the south to north transect, reflecting the sudden, almost threshold-like decline north of Ripon (Figure 3.2, Table 3.7). However, also note that inquiline abundance at the most southern site, Knebworth, was low (Figure 3.2). Five of the 7 sites sampled from east to west in the south of Britain also showed low inquiline abundance. No significant correlations of the geographical variables were found with inquiline abundance along the east to west transect.

Figure 3.2 Mean inquiline abundance (\pm S.E.) plotted against northerliness for each site across the north to south transect

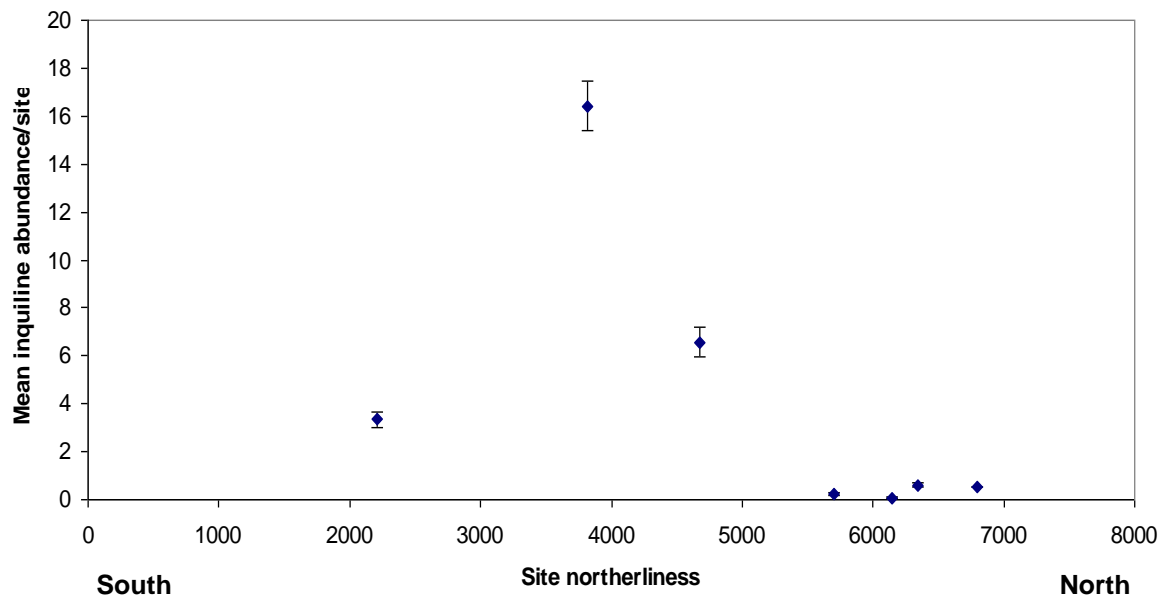


Table 3.7 Significant parameter estimates for inquiline abundance (GLM with normal errors) against geographic location.

Response variable	Explanatory variable	Coefficient	F Ratio	d.f.	P value
Inquiline abundance (north to south)	ln(northerliness)	0.0635	11.52	1, 3	P = 0.04

Inquiline survival

Table 3.8 shows summary statistics for all significant terms of inquiline survival. The relationship between inquiline survival and easterliness across the east to west transect is shown in Figure 3.3. Inquiline survival is significantly higher at the western end of the transect and declines steeply eastwards before levelling out at the eastern end of the transect. The relationship between inquiline survival and northerliness across the north to south transect is shown in Figure 3.4. The proportion of inquilines surviving is significantly higher in the north. No parasitoid attack of inquilines was recorded at Falkirk or Alnwick.

Table 3.8 Significant parameter estimates for inquiline survival (GLM with binomial errors and logit link) against geographic location.

Response variable	Explanatory variable	Coefficients	F Ratio	d.f.	P value
Inquiline survival (east to west)	easterliness	-0.0000408	5041.1	1,3	0.0002
	easterliness ²	0.0000407	1491.6	1,3	0.0007
Inquiline survival (north to south)	northerliness	0.0000263	208.1	1,4	0.005
	northerliness ²	-0.0000206	7622.4	1,3	<0.0001

Figure 3.3 The proportion of inquilines surviving plotted against easterliness for each site along the east to west transect.

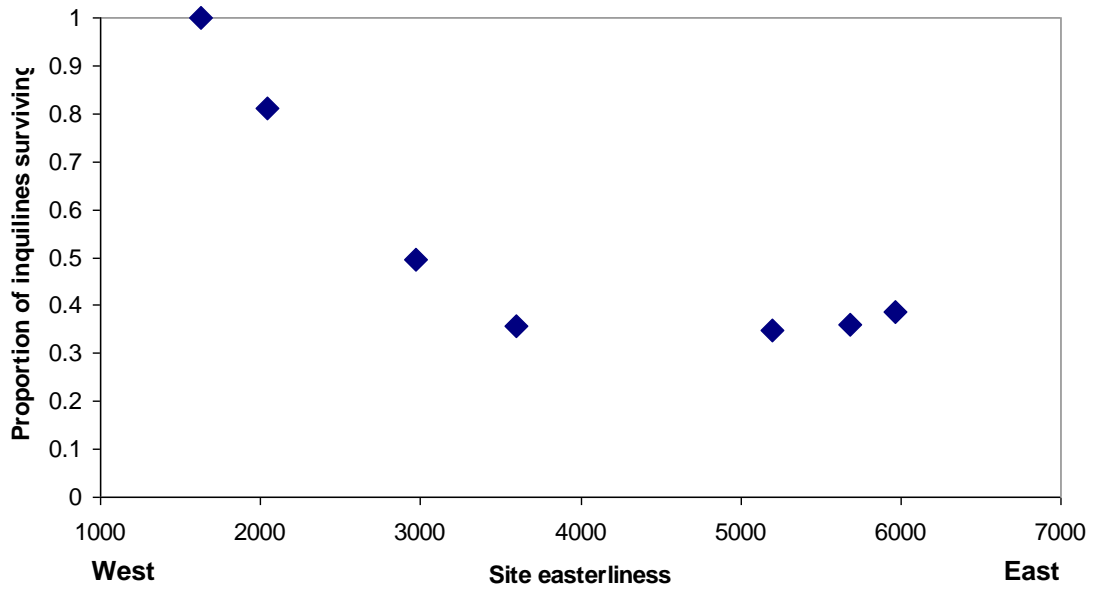
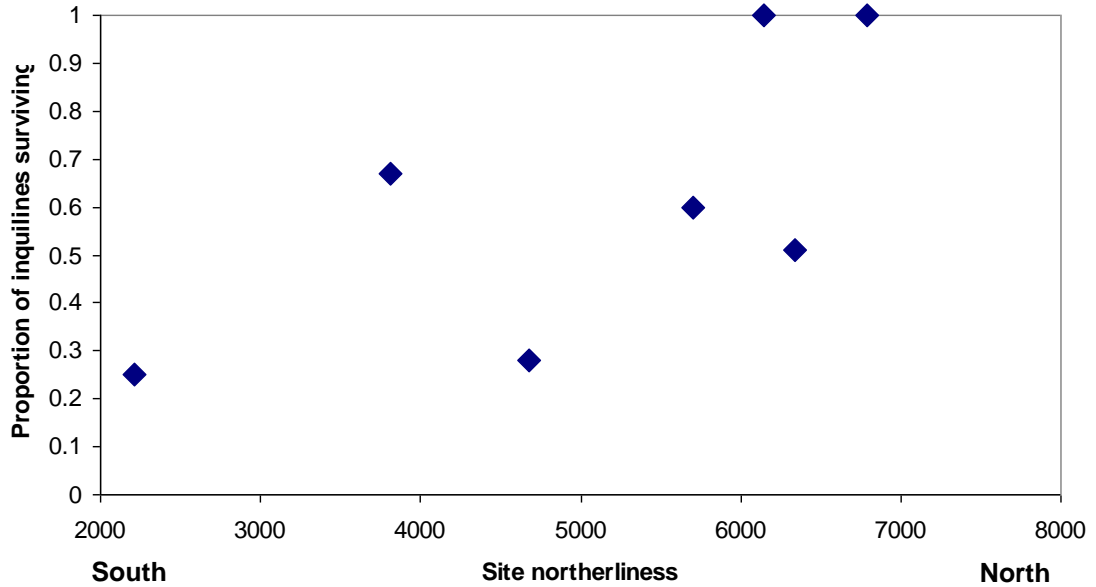


Figure 3.4 The proportion of inquilines surviving plotted against northerliness for each site along the north to south transect.



Parasitoid abundance (outer gall)

No significant correlations of the geographical variables were found with parasitoid abundance across either transect.

Parasitoid species richness (outer gall)

Significance of geographical location for parasitoid species richness was carried out. No terms were found to be significant on either transect including the significance of any relationship between sample size and species richness.

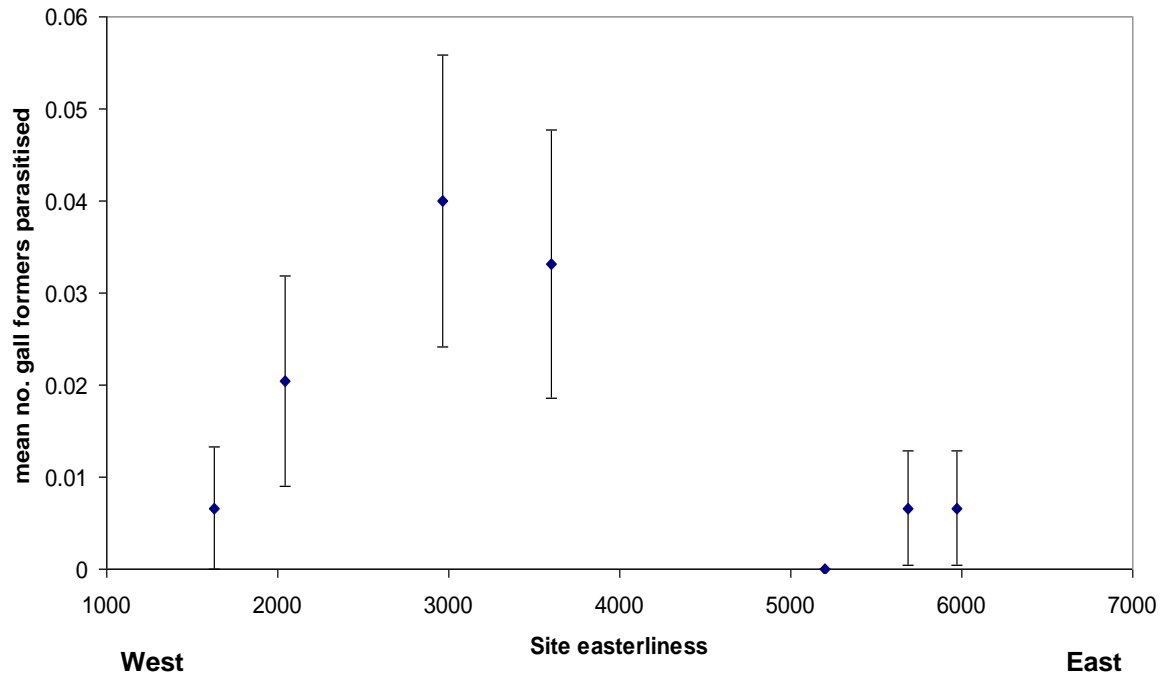
Parasitoid attack of the gall-former (inner gall)

Table 3.9 shows summary statistics for all significant terms for parasitoid attacks of the gall-former. The relationship between parasitoid attack rate of the gall-former and location along the east to west transect is shown in Figure 3.5. Attack rates are significantly lower towards the east and west end of the transect and higher at Yeovil and Dawlish, towards the middle of the transect. No parasitoids attacked the gall-former at Horsham. In contrast, none of the geographical variables were found to be significant for the north - south transect. The number of parasitoid attacks of the gall-former was very low across the north - south transect ($n = 7$).

Table 3.9 Significant parameter estimates for parasitoid attacks of the gall-former (GLM with normal errors) against geographic location.

Response variable	Explanatory variable	Coefficients	F Ratio	d.f.	P value
Parasitoid attacks on the gall-former	easterliness	-59.494	3539.5	1,2	0.011
	easterliness ²	-60.144	3617.3	1,2	0.011

Figure 3.5 Mean parasitoid attack rate of the gall-former (\pm S.E.) plotted against easterliness for each site along the east to west transect.



3.4 Discussion

This study shows that significant changes in the range of the asexual galls of *A. quercuscalicis* and the community associated with the galls have occurred in Britain over the last 15 years. *Andricus quercuscalicis* has expanded significantly northwards (approximately 122 km), spreading at an average linear distance of 8 km yr⁻¹, a moderately slow rate of range expansion compared with some invading cynipid species in Britain, for example, *A. lignicolus* (24.4 km/year) (see Chapter 2, Table 2.2). The last comprehensive survey of *A. quercuscalicis* was conducted during 1991/2 (Schönrogge *et al.*, 1995; 1996). At that time, the distribution of the species was found to extend across southern England from Kent to Cornwall and was abundant almost everywhere that it was recorded in southern England. The most northerly record for *A. quercuscalicis* at that time was Alnwick, Northumberland where, in contrast, only a few individual knopper galls were recorded. The species was found to be sporadic and rare across northern England (Schönrogge *et al.*, 1995; 1996).

The expanding distribution of *A. quercuscalicis* across Britain has, in turn, affected the recruitment of the inquiline *S. gallaepomiformis*. The last survey in 1991/92 (Schönrogge *et al.*, 1995; 1996) showed that distribution of *S. gallaepomiformis* was largely restricted to south east England with sporadic records for Dorset, South Wales and Lancashire. The most northerly record for *S. gallaepomiformis* was from an asexual gall of *A. quercuscalicis* in 1991/92 and was from the Morecambe Bay area, Lancashire (Grid ref. SD 341479) (Schönrogge *et al.*, 1996). The range where *S. gallaepomiformis* attack knopper galls has now expanded significantly northwards (approximately 280 km) extending with an average linear distance of 18.7 km yr⁻¹, over twice the distance that their host, *A. quercuscalicis* has moved north during the same 15 year period. The northern limit of high *S. gallaepomiformis* infestation rates (more than or equal to 1 inquiline per gall) has also moved a comparable distance. Previous studies show the most northerly site with high inquiline infestation was Westleton near Great Yarmouth, East Anglia (Schönrogge *et al.*, 1996). In this study, high infestation rates were found as

far north as Ripon in North Yorkshire, therefore the boundary for galls with a high inquiline infestation has moved an average linear distance of 15.5 km yr^{-1} , almost twice the linear distance for the gall-former (8 km yr^{-1}). Analyses of geographical trends show that inquiline survival is higher at the inquiline invasion front along both the east to west and north to south transects i.e. to the west and north of Britain. By extending its range, an invading species may leave its natural enemies behind and enter enemy-free space (Holt, 1977; Jeffries and Lawton, 1984; Holt and Lawton 1993), before sooner or later being discovered and exploited. In this case, inquilines associated with *A. quercuscalicis* are in enemy-free space at their invasion front before eventually being attacked by parasitoids.

The temporal and geographic pattern of the inquiline increase (Hails and Crawley, 1991; Cornell and Hawkins, 1993; Schönrogge *et al.*, 1996) suggests three possibilities: 1) micro-evolution and adaptation by the inquiline to the new resource (Schönrogge *et al.*, 1996), 2) an increase of encounter frequencies with the increase in host densities (Southwood, 1961; Strong *et al.*, 1984) or 3) pursuit of the host by well adapted genotypes of the inquiline (Hayward and Stone, 2006). These 3 hypotheses are to some extent compatible. That *A. quercuscalicis* may impose selection on inquiline populations is supported by the fact that the emergence time of *S. gallaepomiformis* from knopper galls (July to August) differs from the 2 to 3 generations recorded for this inquiline each year in other cynipid host galls (Askew, 1961; Eady and Quinlan, 1963; Wiebes-Rijks, 1979; Nieves-Aldrey and Villar, 1986). This emergence pattern means that these inquilines do not have to rely on the presence of further host species for a second generation, but can exist using only knopper galls (Schönrogge *et al.*, 1996). Pursuit could involve either native range populations of inquilines, following *A. quercuscalicis* northwards across Britain as a continuation of pursuit across the channel, or pursuit could be by locally adapted populations of southern British inquilines, in a more regional process. Hypotheses concerning the origin of inquilines attacking *A. quercuscalicis* could be discriminated using population genetic approaches (Hayward and Stone, 2006). All 3 hypotheses would predict that 15 years after the last detailed

study, the geographical distribution of the range with high infestation rates should have increased, as has been demonstrated.

The northwards recruitment of inquilines has resulted in a change in the species composition and diversity of the parasitoid complex, which together with the spread of high inquiline abundance, fulfils the first prediction (see Section 3.1, Introduction). This change was first observed by Schönrogge *et al.* (1996) in southern England and occurs because some species of parasitoid, such as *Mesopolobus sericeus* and *Eurytoma brunniventris*, concentrate their attacks on inquilines of knopper galls.

Parasitoid attack of the asexual generation of the gall-former is very low (<6%), 25 years after the first record of attack (Askew, 1961; Schönrogge *et al.*, 1996). In fact, in this study, attack levels are considerably lower than recorded in previous studies (<0.01% north to south transect, 2% east to west transect). These low attack rates contrast strongly with attack rates of parasitoids attacking inquilines in the outer gall wall (33.54% average over samples from 13 sites where parasitism was detected).

Compared with a similar survey of the *A. quercuscalicis* community conducted in 1991/2 (Schönrogge *et al.*, 1995; 1996), the richness of chalcid parasitoid species attacking knopper galls remains the same, at 10 species. However, some key changes in community composition have occurred since 1991/2. *Cecidostiba fungosa* has become an abundant and widespread parasitoid in the community, recorded attacking both inquilines in the outer gall and the gall-former in the inner gall. *Mesopolobus sericeus*, a very localised parasitoid in previous studies, now has a more widespread distribution (Schönrogge *et al.*, 1996). Additionally, as alluded to above, attack rates differ from those recorded in previous studies. *Cecidostiba semifascia* was absent in this study but was recorded as a community member in 1991/92 (Schönrogge *et al.*, 1996). However, this species was rare in 1991/2, and was not reared during earlier (pre-1991) community studies of *A. quercuscalicis* in Britain (Askew, 1961; Hails *et al.*, 1990). In this study, *M. sericeus* had the highest attack rate of those parasitoids attacking the gall-former.

This also represents a change since 1991/92, when *S. biguttata* had the highest attack rate of parasitoids attacking the gall-former.

As in 1991/92 (Schönrogge *et al.*, 1996), all but one species are now more abundant than recorded in the first study of the parasitoid assemblage of *A. quercuscalicis* asexual galls (Hails *et al.*, 1990). The exception of *M. amaenus* has remained unchanged over the last 15 years. The attack rates of parasitoids attacking inquilines in the outer gall have more than doubled over the last 15 years (33.54 % average over samples from 13 sites where outer gall parasitism detected, compared with 15.62% from 38 sites in 1991/92).

Analyses of geographic trends support the prediction that inquiline abundance is higher in the south where *A. quercuscalicis* has been established longer. However, my data do not support the two predictions of higher parasitoid richness and abundance to the south or east. This may be because the parasitoid assemblage associated with knopper galls in northern England has now converged on that found at more established sites in the south. The fact that parasitoids appear very quickly after inquilines become established within knopper galls (Schönrogge *et al.*, 1996) gives some support for this hypothesis.

This study shows that while there have some changes in the community associated with asexual *A. quercuscalicis* galls in Britain, the prediction that the parasitoid and inquiline community of the asexual galls in the invaded range has continued to converge on that of the native range with increasing residence time of *A. quercuscalicis* in Britain is not supported. The community associated with asexual *A. quercuscalicis* galls in Britain is a subset of those species recorded from the gall in the long-invaded and native range in continental Europe and may originate from the local species pool already available in Britain. In order to provide real evidence of convergence, new parasitoid species would need to be recorded from knopper galls, i.e. species which are included in the parasitoid and inquiline community of the gall in continental Europe, but have not been recorded before in Britain, however, such an event may be constrained by the rarity of some species recorded from *A. quercuscalicis* in the native range (see below).

One possibility that may limit convergence of the parasitoid assemblages in the invaded range of Britain with that of the native range is that all the species that are known to attack the galls that are present in the species pool in Britain have been recruited. Examination of the literature does provide some support for this hypothesis. In the native range of *A. quercuscalicis*, a total of 44 species of parasitoids and inquilines have been recorded compared with 25 from Britain. Although not all species known to attack the gall in the native range that are present in Britain have been recruited, most of the remaining species have only rarely been recorded from the gall in the native range and therefore may not typically constitute part of the parasitoid assemblage associated with knopper galls. Additionally, several of these same species are only rarely recorded from cynipid galls native to Britain. This species complex includes the inquilines *Ceroptres clavicornis*, *Synergus crassicornis*, *Synergus incrassatus* and *Synergus reinhardi* of which only one specimen of each has been recorded to date from knopper galls in the native range (Mayr, 1872; Pfützenreiter and Weidner, 1958; Diakontshuk and Melika, 1993; Pujade-villar *et al.*, 2003) and *Synergus pallidipennis*, known from only five specimens reared from knopper galls collected in Hungary (Pujade-villar *et al.*, 2003).

Similarly, many species within the potential parasitoid species pool in Britain have rarely been recorded from the parasitoid assemblage in the native range. These include *Sycophila variegata* (2 specimens), *Hobbya stenonata* (1 specimen) (Pujade-villar *et al.*, 2003), *Mesopolobus fasciiventris* (1 specimen) (Mayr, 1903), *Aulogymnus skianeuros* (1 specimen) and *Aulogymnus gallarum* (5 specimens) (Pujade-villar *et al.*, 2003). Conversely, some species are regularly recorded as part of the parasitoid assemblage in the native range but are rare species within the British parasitoid species pool. These include *Aulogymnus trilineatus*, in the UK only recorded from *Andricus foecundatrix* asexual galls (4 specimens), one *Andricus kollari* asexual gall (1 specimen) (Askew, 1961), *Ormyrus pomaceus*, only recorded from *A. corruptrix* asexual galls (2 specimens) (Schönrogge *et al.*, 2000) and *Biorhiza pallida* sexual galls (1 specimen) (Askew, 1961) in Britain. Only one species of parasitoid, *Baryscapus pallidae*, has been recorded regularly from knopper galls in the native range and has also been regularly recorded

from the potential parasitoid species pool in Britain (*B. pallida* sexual galls in Britain) (Graham, 1991), however, this parasitoid has yet to discover and exploit knopper galls in Britain.

As previously discussed (see Section 3.1, Introduction), the development of the community prior to this study could be considered to have occurred in two phases, the first being a substantial species turnover resulting in changes in species composition (Hails *et al.*, 1990; Schönrogge *et al.*, 1994; 1995; 1996) and the second, a pronounced change in the abundance of inquilines in south east England (Schönrogge *et al.*, 1996). Subsequently, parasitoid species attacking the inquilines increased in distribution and abundance. The current status of the British community suggests that after initially increasing in similarity to the native range, the number of species recorded has stabilised with no increase in species richness being recorded over the last 15 years.

Cornell and Hawkins (1993) reviewed the recruitment of parasitoid species for many phytophagous invading insect species in a comparative analysis. They found that the time over which the invader kept recruiting parasitoid species was variable. After controlling for host vulnerability and sample size, residence time made no significant contribution explaining parasitoid recruitment, but is described by the authors as encounter frequencies (Strong *et al.*, 1984; Cornell and Hawkins, 1993). Recruitment was described as a relatively continuous process determined by periods of time that individual parasitoid species need to adjust to the new host, and/or by the progressing invasion which might bring the invader in contact with more parasitoid species and larger numbers of individuals of common, widespread parasitoids (Schönrogge, 1994). Three hypotheses may explain the limited recruitment of new parasitoid species to knopper galls in Britain over the last 15 years, none of which are mutually exclusive: 1) the limitations imposed by the available parasitoid pool that could potentially attack knopper galls in Britain could slow down the rate of species recruitment; 2) species that attack knopper galls in the native range, but where British populations are naïve to the new hosts, might recruit more slowly; 3) common and widespread parasitoids in Britain

that were not previously recorded from the parasitoid assemblage of knopper galls in the native range may require a bigger adaptive leap in order to exploit and attack knopper galls in Britain.

Chapter 4

An assessment of the ecological impact of invading oak gallwasps in Britain using quantitative webs

4.1 Introduction

There is considerable interest in the impacts of biological invasions of both plants (Strong *et al.*, 1984) and animals, notably phytophagous insects (Cornell and Hawkins, 1993) on native communities. Within their invaded range, an invading species may interact directly or indirectly with an existing community of species. Both types of interaction can structure biological communities by affecting the identity, number and abundance of species present (Morris and Lewis, 2002). While direct interactions such as predation and competition may be readily observed, indirect interactions, including apparent competition, are inherently difficult to identify in field situations (Holt and Lawton, 1994; Schönrogge and Crawley, 2000).

Apparent competition is defined as a negative effect of one species on the population growth rate or abundance of another species, mediated through the action of shared natural enemies (Holt and Lawton, 1993; Morris *et al.*, 2004). Theory suggests that apparent competition may be a particularly important force structuring communities of phytophagous insects in host-parasitoid systems (Holt and Lawton, 1993, Morris and Lewis, 2002). This is largely because parasitoids usually have a generation length comparable to that of their hosts, so the numerical response by the parasitoid population

can occur on the same time scale as host recruitment (Holt and Lawton, 1993). Additionally, parasitoids have the capacity to sharply reduce host densities well below the carrying capacity set by resources (Hawkins and Lawton, 1987; Hawkins, 1988; 1990; Holt and Lawton, 1993).

Originally, food webs (i.e. binary or qualitative webs) were used as a graphic illustration of trophic relationships in communities (community webs), or a given group of species with a focal species at the lower trophic level (source webs), or at the higher trophic level (sink webs). Semi-quantitative webs include some quantitative data on the relative frequency of natural enemies attacking phytophagous insects, but not data on the relative abundances of the herbivores themselves (van Veen *et al.*, 2006). Most recent studies have used fully quantitative webs, which estimate absolute population densities for a given area of all species involved together with absolute attack rates (Memmott and Godfray, 1994; Memmott *et al.*, 1994; Müller *et al.*, 1999; Schönrogge and Crawley, 2000; Rott and Godfray, 2000; Valladares, *et al.*, 2001; Lewis *et al.*, 2002; Willis and Memmott, 2005). These quantitative webs are essential to assess the potential importance of apparent competition between species within communities, to determine the strength of trophic links between species (Montoya *et al.*, 2006) and therefore help build on existing knowledge about community structure and function.

In 1994 and 1995, cynipid gall communities at 8 sites in Britain were studied intensively to produce quantitative webs (Schönrogge and Crawley, 2000), as previously discussed in Chapter 1 (Section 1.7). The main feature of all 8 communities found during this study was the absence of links between parasitoid assemblages centred on the sexual generation galls of the invaders on *Q. cerris* and the assemblages on native oaks attacking native gallwasps and the sexual generations of the invaders (Schönrogge and Crawley, 2000).

Since Schönrogge and Crawley's study (2000), significant changes have occurred in the distribution and species richness of cynipid galls within Britain (Chapters 2 and 3,

Figures 2.2 and 2.3). Notably, 8 new invading cynipid species have been recorded in the UK: *A. lucidus* (Stone & Sunnucks, 1992), *Aphelonyx cerricola* (Crawley, 1999), *A. aries* (Leach & Shirley, 1999), *A. grossulariae* (Walker, 2001), *Plagiotrochus quercusilicis* (Hancy & Hancy, 2004), *Neuroterus saliens* (Redfern, 2006), and both *P. coriaceus* and *P. australis* (Robbins, 2007). The more established invaders such as *A. quercuscalicis* and *A. lignicolus* have shown continued range expansion both north and west of the ranges recorded in 1991/92 (Chapters 2 and 3).

In this chapter, I present quantitative webs for a guild of multiple native species, 4 longer-established invading gallwasps first recorded between the mid 19th century and the mid 1970's, and 4 of the most abundant and widespread recent invaders (*A. lucidus*, *A. aries*, *A. grossulariae* and *Aphelonyx cerricola*). The remaining 4 recent invaders are rare and restricted to their sites of first record, and so are not yet amenable to web-based approaches.

The aim is to compare webs generated before and after the arrival of the 4 more recent invaders and to examine changes in community structure and function that may have resulted as a consequence of the establishment of these 4 additional cynipid hosts. More specifically I ask: (1) Have attack rates for parasitoids of invading gallwasps changed over the last 10 years? (2) Has the arrival of new invasive species altered the extent to which parasitoid communities focused on native and invading gallwasps interact? (3) Is apparent competition currently important in structuring the cynipid communities?

Through these questions, I will test the following hypotheses:

- That web complexity will reflect the residence times of the invaders where they are sampled. This pattern was demonstrated for *A. quercuscalicis* on a European scale by Schönrogge *et al.* (1995), and for the same species in the UK by Schönrogge *et al.* (1996). In general, this hypothesis predicts fewer trophic links

between species in communities from northern Britain compared with those in southern Britain.

- That shared parasitoids will place the 4 more recent invaders in food web compartments containing other gallwasp generations on the same host oaks. This is based on previous studies showing that parasitoid communities associated with *Q. cerris* are qualitatively and quantitatively distinct from those associated with *Q. petraea* and *Q. robur* (Schönrogge and Crawley, 2000). This is significant, because if this distinction is maintained, it means that only the asexual generations of invading *Andricus* species support parasitoid assemblages capable of interacting with native oak gallwasps. Breakdown of this distinction would broaden the potential for indirect interactions between gallwasp generations on the two oak groups.

To my knowledge, this is the first study to examine changes within communities by comparing quantitative web data collected before and after colonisation by additional invading species. In this case, quantitative web data were first collected in 1994/5 and the results presented in Schönrogge and Crawley (2000). Here I use the same methodology and an overlapping set of sites to construct fully quantitative webs for the years 2005/6, allowing direct comparison with the 1994/5 data.

4.2 Methods

4.2.1. Selection of sites and trees

Four of the original 8 study sites established by Schönrogge and Crawley (2000) for work on the first 4 invaders were used again in this study to maximise compatibility of results (see Chapter 1, Figure 1.5). I included the 2 most southern sites, Puttenham Common (Surrey) and Silwood Park (Berkshire), where 4 recently invading cynipids are known to be established (*A. aries*, *A. grossulariae*, *A. lucidus* and *Aphelonyx cerricola*).

To these I added the 2 most northern sites, at Beaully (Inverness-shire) and Dunrobin Castle (Sutherland). In 1994/1995 only *A. kollari* was recorded at Dunrobin. *A. lignicolus* is also now present at this site (Chapter 2). For each of these 4 sites, the distribution and size structures of the oak stands are given by Schönrogge *et al.* (1998) and are reproduced in the Appendix (Appendix Table 7.2).

4.2.2. Randomised sampling of shoots

In 2005/6, I sampled 6 trees at random from marked cohorts of suitable *Q. cerris* at the 4 sites. At Puttenham and Silwood, I sampled the same 6 trees used during the 1994 study by Schönrogge and Crawley (2000). Sampling of branches and shoots closely followed methods used by Schönrogge and Crawley (2000), as follows. Samples of 15 branches were taken across all possible aspects and heights from each of the selected sample trees using a pole pruner to give a reach of approximately 8 metres. A branch is defined as 4 years of discrete growth, as identified by 4 sets of ring scars counting back along the branch from the shoot tip (Schönrogge *et al.*, 1998). Six shoots (defined as last year's growth) were then chosen at random from every branch and the number of galls and buds, either intact or predated, were counted, giving a total of 90 randomly selected shoots per tree. This sampling scheme also established the branching pattern in the outer canopy of the trees in order to estimate absolute gall densities for quantitative webs (see Section 4.2.5. below). Bud galls of invading cynipid species on *Q. cerris* are very small and concealed within the buds, therefore *Q. cerris* shoots were taken back to the laboratory for dissection.

4.2.3. Gall collection and rearing

The phenology of spring gall development required a first collection from *Q. cerris* in mid to late April. At this time, buds were dissected for density estimates of *A. lignicolus*, *A. kollari* and *A. corruptrix* sexual generations. A second collection was made in mid to late May to estimate the densities of *A. quercuscalicis* and *A. grossulariae* sexual

generations. Catkin galls of *A. quercuscalicis* were sampled for rearing at this time, while *A. grossulariae* galls were sampled when suitably mature at the beginning of June, together with sexual generation galls of native cynipids on *Q. robur*/*Q. petraea*. Most parasitoids attacking these galls are late instar or pupal parasitoids, and the galls were thus collected as late as possible in order to avoid missing parasitized galls by collecting too early. The density census for asexual generation galls was taken in early August before galls reach maturity. This avoids underestimating gall densities as some galls drop off the host tree upon maturation.

Galls found in *Q. cerris* buds and catkins during dissection were reared in small glass tubes. Native oaks (*Q. robur* and *Q. petraea*) were searched at each site for 4 person-hours and all gall species collected. Where possible, and with exceptions detailed below, 150 galls of each species were collected from each site for rearing. Sample sizes reared for web construction for all species at each site are given in Table 4.1. A sample size of 150 galls is sufficient to rear most of the parasitoid assemblage associated with any given gall type (McArdle, 1990, Schönrogge, 1994). Where more than 150 galls were collected, a sub-sample of 150 galls was taken to allow direct comparison of species richness between sites and with earlier work by Schönrogge and Crawley (2000). Any excess galls were reared and in none of the rearings did the increase in sample size result in an increase in the number of parasitoid and inquiline species. For cynipid galls where rearing mortality is often high (e.g. *Neuroterus* sp. 'spangle gall' asexual generations), a sample size of up to 1000 galls in each rearing was used. For rare species, all galls found were reared, in some cases this number being much less than 150 galls (see Table 4.1). All rearings were stored in an outside insectary and emerging adult gallwasps, inquilines and parasitoids were collected weekly and parasitoids were identified using appropriate keys (Askew and Thúroczy, in prep; Pujade-Villar and Nieves-Aldrey, in prep). Sub samples of parasitoid species were sent to Dr R. R. Askew (UK) to confirm correct and consistent identification. Inquiline identification is difficult, and all inquilines were therefore sent for identification by a specialist taxonomist (Dr. G. Melika, The Plant Protection and Soil Conservation Service of County Vas, Hungary).

4.2.4. Pairwise interactions via parasitoids and inquilines

The potential for pairwise indirect interactions from generation to generation, i.e. the gall types of each generation of the galler species are treated as separate entities, was assessed as in the analyses of the 1994/5 study (Schönrogge and Crawley, 2000) using the following measure:

$$d_{ij} = \sum_k \left[\frac{\alpha_{ik}}{\sum_l \alpha_{il}} \frac{\alpha_{jk}}{\sum_m \alpha_{mk}} \right]$$

This quantifies the possible interactions between two hosts via all shared parasitoids and asks what fraction of the parasitoids attacking gall species i were also found in gall species j . If this fraction is high, the indirect effect of host i on j is possibly great.

α_{ik} is the strength of the link between host i and parasitoid k in the quantitative web.

d_{ij} summarises the interactions between two hosts via all shared parasitoids, and thus the outer summation is taken over all parasitoid species (Müller *et al.*, 1999; Schönrogge *et al.*, 2000).

The first term in the square brackets is the fraction of parasitoids of host i that belong to species k and the second term is the fraction of parasitoids of species k that were also found in gall species j . If two galls i and j share no parasitoid or inquiline species, then $d_{ij} = 0$. If species i is attacked by one or more parasitoid species that show high attack rates in host j , then $d_{ij} = 1$, which would constitute a very strong interaction, particularly if host j is very abundant (Schönrogge *et al.*, 2000).

4.2.5. Quantified webs and linkage diagrams

To express species densities per area, and so allow comparison of webs between sites, and of the 94/95 webs with those collected in 05/06, I employed the same method described by Schönrogge *et al.* (1998; 2000). Gall density per shoot was measured directly and established the branching pattern in the outer canopy of the trees (see Section 4.2.2. above) and total numbers of galls per tree were estimated as follows. In order to establish the branching order in the inner canopy, for each tree I summarised tree architecture through a ‘trunk score’. Six main branches were followed from 3 year old growth towards the tree trunk and the number of binary branching points counted. The number of shoots in a tree was estimated as: $N_{\text{shoots}} = 2^{n-2}(\text{shoots/twigs})^2$, where n is the branching score for the trunk of the tree. The mean number of galls per shoot multiplied by N_{shoots} is the estimated number of galls on a sample tree. The number of galls per 100m² is the average number of galls over all sample trees multiplied by the number of host trees (*Q. cerris* vs *Q. petraea/robur*) per 100m² and weighted by tree size (Schönrogge *et al.*, 1998; 2000). Parasitoid and inquiline densities per 100m² were calculated for each species by multiplying host gall densities by their respective attack rates as established in the rearings (see Chapter 3 for explanation of attack rate calculation). Parasitoid and inquiline densities per 100m² for all webs are shown in the Appendix (Table 7.3).

The 6 quantitative webs in Figures 4.1a-f show the quantified associations between inquilines, parasitoids and their cynipid hosts for the spring and autumn generations 2005 (Figures a-d, all sites) and the autumn 2005 and spring 2006 generations (Figures e-f, Silwood and Puttenham only). The webs contain only those species from which parasitoids or inquilines emerged and by definition include only those species whose abundances were above detectable densities in random sampling. Webs were drawn using QWeb software designed by K. Schönrogge (2007).

In each web, the top bar (red) represents parasitoid species. The bottom bar (blue) represents inquiline species. The central bar (green) represents gall inducer species. The gall inducer species in each web are presented from the left to right in the same order in which they are listed in the figure legend. Parasitoids and inquilines are identified by numbers and a key is given in each figure. For each trophic group, the proportion of the total width of the bar occupied by a given species is proportional to its abundance. To allow total bar width for each trophic group to be the same, the parasitoid and inquiline abundances have been scaled relative to the host by factors given next to each bar.

Figures 4.2a-f show social networks for the cynipid communities and their links via shared parasitoids for the 4 sites. Images were produced using UCInet software (Borgatti *et al.*, 2002). These networks, in contrast to the webs, feature only the gallwasp hosts. Placement of host generations is dictated by dissimilarities in parasitoid community assemblage composition and the relative abundance of shared parasitoids and inquilines. Dissimilarities between the parasitoid communities associated with the galls repel and are represented in geodesic distances between hosts in the network. Links between the galls indicate that they share parasitoid species and their strength (the width of links between cynipid species) indicates the mean contribution between the partners. The nodes in the networks represent the cynipid hosts, identified with a consistent set of abbreviations as follows: Acor – *A. corruptrix*, Acur – *A. curator*, Ak – *A. kollari*, Alig – *A. lignicolus*, Aqc – *A. quercuscalicis*, Aquad – *A. quadrilineatus*, Bp – *Biorhiza pallida*, Cdiv – *Cynips divisa*, Clong – *C. longiventris*, Nalb – *Neuroterus albipes*, Nant – *N. anthracinus*, Nn – *N. numismalis*, Nqb – *N. quercusbaccarum*, Asol – *A. solitarius*, Agr – *A. grossulariae*, Afec – *A. fecundator*, Aaries – *A. aries*. Square symbols annotated with -a represent the asexual generation and circles annotated with -s, the sexual generation. Symbol size scales with host gall densities per unit area (100m²). The symbol colour indicates whether the galls are UK invaders (red) or natives (blue).

4.3 Results

4.3.1. Host species richness and abundance

The cynipid species recorded at each of the 4 sites are shown in Table 4.1. Gallwasp species richness is higher in the southern webs than in the northern webs, largely because the 4 recently invading gallwasp species make a significant contribution to the southern webs and are currently restricted to southern England (see Chapter 2). All 8 sampled invading gallwasp species account for 47% of all species recorded in the southern webs, compared with 20% in the northern webs.

Table 4.2 shows the parasitoid and inquiline species recorded at each of the 4 sample sites. As with cynipid species richness, parasitoid and inquiline species richness was higher in the southern than the northern webs, with about 3 times as many parasitoid species in the southern webs compared to the northern webs.

Each cynipid species was ranked according to its absolute abundance at each of the 4 sites (Table 4.3). In spring 2005, *Andricus quercuscalicis* was by far the most abundant cynipid species at the 2 southern sites (Silwood and Puttenham). At these sites, invading cynipid galls dominated the spring communities and were far more abundant than native galls. At the 2 northern sites, the native species *Andricus quadrilineatus* was the most abundant species at Beaulieu, and the invading species *A. lignicolus* was most abundant at Dunrobin. In autumn 2005, *Neuroterus quercusbaccarum* was by far the most abundant species at all 4 sites, the density being highest at Beaulieu, although the density of *N. quercusbaccarum* at Dunrobin was very low relative to the other sites (Table 4.3). In contrast to the spring cynipid communities, native species dominated the autumn communities at all sites and invading species were generally less abundant. Large changes in gall abundance were found between spring collections made at Silwood and Puttenham in 2005 compared with 2006. At Silwood, densities of the invading cynipids *A. quercuscalicis*, *A. lignicolus* and *A. grossulariae* declined by one order of magnitude

(Table 4.3). Fluctuations in native gall densities were also large, with *N. quercusbaccarum* declining by 2 orders of magnitude in 2006 (Table 4.3). Similar fluctuations in gall density were recorded at Puttenham, where *A. kollari* declined by 2 orders of magnitude in 2006 and *A. corruptrix* declined by one order of magnitude (Table 4.3). Notably, *B. pallida* was not recorded at either Silwood or Puttenham in 2005 but was abundant in 2006.

4.3.2. Webs for the south of Britain – Silwood and Puttenham

At Silwood, all 8 of the invading cynipid species studied were present, although of the recent invaders, *A. aries*, *A. lucidus* and *Aphelonyx cerricola* were rare and not recorded during random sampling of branches. No parasitoids or inquilines emerged from rearings of these 3 species collected at Silwood and they are not included in the quantitative web (Figure 4.1a). At Puttenham, 6 of the invading species were recorded. *Andricus lucidus* and *Aphelonyx cerricola* were absent, and *A. kollari* and *A. aries* were rare, with no parasitoids emerging. These 4 species are thus absent from the quantitative web (Figure 4.1b). Parasitoid densities for all webs are given in the Appendix, Table 7.3.

The spring sexual generations

(a) Natives

The species richness of sexual generation native galls was low in both spring 2005 and spring 2006 and the species composition at both Silwood and Puttenham also changed from 2005 to 2006. In spring 2005, 3 native cynipid species produced parasitoids: *A. curvator*, *N. quercusbaccarum* and *N. numismalis*. *Neuroterus quercusbaccarum* produced the greatest richness of parasitoid species in spring 2005, yielding 7 parasitoid species (Table 4.2). The sexual generation galls of *B. pallida* were rare in 2005 but more abundant in 2006 and this species was the only native sexual gall that produced

parasitoids in 2006. The greatest richness of parasitoid species from all cynipid galls recorded was reared from *B. pallida*, which produced 14 species of parasitoids in 2006.

(b) Invaders

Rearings of the sexual spring generations of the invading species (with the exception of *A. grossulariae*) produced parasitoids but no inquiline species. The cynipid species *A. corruptrix*, *A. kollari* and *A. lignicolus* yielded only one parasitoid species, *Mesopolobus fuscipes*. In 1995, an additional species, *M. dubius*, was recorded from *A. corruptrix* and *A. kollari* while in addition to these 2 species, *M. xanthocerus* was recorded from *A. lignicolus*. The catkin galls of *A. quercuscalicis* from Silwood produced 5 species of *Mesopolobus* parasitoids in spring 2005 (*M. fuscipes*, *M. tibialis*, *M. xanthocerus*, *M. dubius* and *M. sericeus*, together with *C. fungosa* and *Ormocerus vernalis* (*O. vernalis* represented by one specimen only). The same parasitoids were recorded in spring 2006 with the exception of *M. sericeus* and *O. vernalis*, which were not recorded. In 2005, *A. quercuscalicis* from Puttenham yielded four *Mesopolobus* species: *M. fuscipes*, *M. tibialis*, *M. xanthocerus*, *M. dubius* and all except *M. dubius* in spring 2006 in addition to the parasitoid *C. fungosa*. The parasitoids *M. tibialis* and *M. fuscipes* accounted for more than half of all parasitoid emergence at the southern sites, predominantly from the invaders *A. quercuscalicis*, *A. corruptrix* and *A. grossulariae*.

The cynipid species *A. corruptrix*, *A. kollari* and *A. lignicolus* yielded only one parasitoid species, *Mesopolobus fuscipes*. This is a reduction in the richness of parasitoid species recorded in 1995. Compared with 1995 quantitative webs (Schönrogge and Crawley, 2000), parasitoids attacking *A. quercuscalicis* catkin galls have increased in richness with 3 additional species of parasitoid being recorded (*C. fungosa*, *M. sericeus* and *O. vernalis*). The recent invader *A. grossulariae* yielded the greatest richness of parasitoids and inquilines of any invader (9 parasitoid species and one inquiline, *Synergus gallaepomiformis*), and produced a richness of species second only to native *B.*

pallida. The inquiline *S. gallaepomiformis* is very rare in *A. grossulariae* spring galls and only one individual was reared.

Some significant changes in the attack rates for parasitoids of invading gall wasps have occurred since 1995. The most notable change is in the increase in the attack rates of *M. fuscipes* and *M. tibialis* on the catkin galls of *A. quercuscalicis*. The attack rate of *M. fuscipes* has increased by 3 orders of magnitude when compared with 1995 quantitative webs and *M. tibialis*, which was not recorded from *A. quercuscalicis* in 1995, has become a dominant member of the parasitoid assemblage of *A. quercuscalicis* galls (see Appendix, Table 7.3, parasitoid densities). In 2005/6, only *M. fuscipes* was recorded from the galls of *A. lignicolus*, *A. kollari* and *A. corruptrix* at both Silwood and Puttenham, and therefore significant declines in the attack rates of other parasitoid species previously recorded from these galls have occurred. Species in which attack rates have declined most significantly include *M. xanthocerus* (declined by 4 orders of magnitude) and *M. dubius* (declined by 3 orders of magnitude), recorded in 1995 from *A. lignicolus*.

In the 1995 quantitative webs, the parasitoid communities attacking galls of the invading cynipid species on *Quercus cerris* and native species on *Q. petraea/robur* differed to the extent that no parasitoid species were common to cynipids found on these two oak groups i.e. the gallwasp sexual generations fell into separate trophic compartments based on their host oaks. The 2006 quantitative webs show that there is now considerable overlap between parasitoid communities associated with galls of *Q. petraea/robur* and *Q. cerris* in southern Britain (Figures 4.1a, 4.1b) and there are no longer separate trophic compartments based on host oaks for sexual galls.

In spring sexual generations, *A. grossulariae* and *A. quercuscalicis* are particularly important gall species that link the sexual generations of the invading species on *Q. cerris* to the native galls on *Q. robur* via shared parasitoids. At both Silwood and Puttenham, *A. grossulariae* shares at least 2 parasitoid species with each of the species

of native gallwasp included in the webs. Parasitoids most frequently shared include *M. tibialis* and *T. flavipes*, which *A. grossulariae* shared with *N. quercusbaccarum* and *A. curvator* at Silwood in 2005. Most overlap between parasitoids shared between native and invading cynipids in spring was found between *A. grossulariae* and *N. quercusbaccarum*, which shared 5 parasitoids (*M. tibialis*, *M. fuscipes*, *E. brunniventris*, *T. flavipes* and *Megastigmus dorsalis*) of 6 species that emerged from *N. quercusbaccarum* at Silwood in spring 2005.

The autumn asexual generations

(a) Natives

The native species *N. quercusbaccarum* was the most abundant gall at Silwood and Puttenham but unfortunately no parasitoid or inquiline emerged from the galls and these species are therefore not included in the webs. This was because of difficulties in rearing these galls, which resulted in low emergence rates for all gall inhabitants. Other natives, including *N. numismalis*, *N. anthracinus* and *N. albipes*, were also recorded but yielded only gallwasps and no parasitoids, although one inquiline species, *S. gallaepomiformis* emerged from *N. anthracinus*.

(b) Invaders

Of the 8 invading cynipid species studied (*A. quercuscalicis*, *A. lignicolus*, *A. kollari*, *A. corruptrix*, *A. aries*, *A. grossulariae*, *A. lucidus* and *Aphelonyx cerricola*), only the asexual generation of *A. quercuscalicis* was recorded during random sampling and yielded parasitoid and inquiline species. All other invading species were rare and/or yielded no parasitoids or inquilines.

Where emergence occurred, the asexual generation galls of *A. quercuscalicis* were a focal point of attack for parasitoid and inquilines. This gall type was attacked by 7

species of parasitoid and 2 species of inquiline at Silwood (Figure 4.1a, Appendix Table 7.3) and by 4 parasitoids and 2 inquilines at Puttenham (Figure 4.1b, Appendix Table 7.3). In 1995, asexual generation *A. quercuscalicis* were also attacked by more parasitoid and inquiline species than any other asexual generation gall, although parasitoid species richness was higher overall in 1995 (9 parasitoids and 2 inquilines at Silwood, 10 parasitoids and one inquiline at Puttenham: Figures 4.1a, 4.1b). *Cecidostiba fungosa* was the most abundant parasitoid to emerge and represented 46% of all parasitoids emerging from *A. quercuscalicis* in autumn 2005. In 1995, *C. fungosa* and *E. brunniventris* were the most abundant parasitoids recorded from *A. quercuscalicis* at Silwood. At Puttenham, *C. fungosa* was not reared from *A. quercuscalicis* in 1995 but was reared from *A. corruptrix* (Figure 4.1b). This differs from the situation in 2005 because *C. fungosa* attacked *A. quercuscalicis* at both sites. Comparison could not be made with emergence from asexual *A. corruptrix* galls as none were collected from Puttenham in 2005. *Eurytoma brunniventris*, previously abundant in 1995, attacked *A. quercuscalicis* in low numbers (<1%) in 2005. *Synergus gallaepomiformis* was the dominant inquiline in both 1995 and 2005. This inquiline accounted for over 15% of individuals emerging from *A. quercuscalicis* with small numbers of *S. umbraculus* (<1%) also emerging in 2005.

Comparing the species recorded from *A. quercuscalicis* in 1995 and 2005, the attack rates for most species of inquilines and parasitoids at both Silwood and Puttenham are approximately one order of magnitude less than attack rates recorded in 1995 (Appendix, Table 7.3). No other asexual autumn generation galls produced parasitoids or inquilines from which comparisons of attack rates could be made.

4.3.3. Webs for the north of Britain – Beaully and Dunrobin

Only two of the invading species, *A. lignicolus* and *A. kollari*, were recorded and webs for these northern sites (Figures 4.1c and 4.1d) are much simpler than those in southern England. This results both from reduced cynipid species richness and lower parasitoid

richness, and there are fewer links between species via shared parasitoids in the webs (Figures 4.3c and 4.3d) (For parasitoid densities see Appendix, Table 7.3).

One striking contrast between 1995 and 2005 webs is the dramatic change in invading cynipid gall density. In 1995, *A. kollari* density estimates at Beaulieu and Dunrobin were 22000 and 35000 galls per 100m² respectively (Schönrogge *et al.*, 1999). This contrasts sharply with much lower density estimates recorded in 2005 for *A. kollari*, which were 3 orders of magnitude lower at Beaulieu (31 galls/100m²) and 2 orders of magnitude lower at Dunrobin (117 galls/100m²). Conversely, *A. lignicolus* density at Beaulieu was 5 times higher in 2005 than in 1995, rising from 100 to 500 galls/100m².

Gall densities have consequences for the number of galls that can be reared. Where gall densities are low, it may not be possible to collect a sample size of 150 galls. Consequently, very small sample sizes in rearings can produce only a proportion of the parasitoid assemblage from any given gall type and will not necessarily reflect the species richness of parasitoids of the wider cynipid population.

The spring generations

(a) Natives

Parasitoid and inquiline richness was greater from native cynipid species than invading species. *B. pallida* produced the greatest richness of species with 5 species of parasitoid and one inquiline at Beaulieu (species listed in Appendix, Table 7.3). No *B. pallida* were recorded at Dunrobin, where only 2 native galls yielded parasitoids: *N. quercusbaccarum* produced 4 parasitoids (*M. tibialis*, *M. dubius*, *M. fuscipes* and *T. flavipes*) and *A. curvator*, one parasitoid (*T. flavipes*) (Table 4.2). *Andricus quadrilineatus* was recorded at both sites but only gallwasps emerged from this gall species, and it is therefore not included in the webs (Figures 4.1c and 4.1d).

(b) Invaders

In 1995 at Beaulieu, both *A. kollari* and *A. lignicolus* were collected and only the parasitoid *M. fuscipes* emerged from both gall species. In 2005, although the 2 invading species *A. lignicolus* and *A. kollari* were recorded during random sampling, no parasitoids or inquilines emerged from either species at Beaulieu. Variation in the sample size of galls reared (150 galls in both datasets) does not explain the lack of parasitoid emergence recorded from *A. lignicolus*. However, for *A. kollari*, only 60 galls were reared in 2005 (Table 4.1) due to low gall density and this small sample size could have resulted in no parasitoid emergence being recorded, particularly if parasitoid density was low in the wider cynipid population. In 1995 at Dunrobin, only *A. kollari* was recorded. By 2005, *A. lignicolus* had expanded its range northwards and was recorded at Dunrobin, together with *A. kollari*. In both 1995 and 2005, only *M. fuscipes* emerged from *A. kollari* at Dunrobin. This was also the only parasitoid to emerge from *A. lignicolus* at this site in 2005 (Table 4.2).

With the exception of the parasitoid *M. fuscipes* that emerged from both the invading species (*A. lignicolus* and *A. kollari*) and *N. quercusbaccarum* at Dunrobin, the parasitoid communities in 2005 attacking galls of the invading cynipid species on *Q. cerris* and *Q. robur* were compartmentalised (Figures 4.1c and 4.1d) as they were found in 1995. More *M. fuscipes* emerged from invading than from native galls, but the attack rates for all parasitoids for all gall species were very low (see Appendix, Table 7.3 for parasitoid densities).

The autumn asexual generations

As discussed, the webs are much simpler for the northern sites than the southern sites but unlike the autumn generations in southern Britain, the asexual generations of the invaders *A. kollari* and *A. lignicolus* were the only species that produced parasitoids and inquilines.

(a) Natives

The native *N. quercusbaccarum* was found in very high densities at Beaully (Table 4.3, Figure 4.1c, Appendix, Table 7.3). Although *N. quercusbaccarum* was also the most abundant gall at Dunrobin, the density of galls for all species at this site was very low (Table 4.3, Figure 4.1d, Appendix, Table 7.3). Unfortunately, as at Silwood and Puttenham, no parasitoids or inquiline emerged from these species and they are not included in the webs. Again, this is associated with difficulties in rearing parasitoids from this gall.

(b) Invaders

At Beaully in 2005, *A. kollari* produced one inquiline, *S. umbraculus*, and 3 species of *Torymus*: *T. auratus*, *T. flavipes* and *T. geranii* (Table 4.2). Only *T. auratus* emerged from *A. lignicolus*. At Beaully in 1995, no autumn asexual generation galls of *A. kollari* or *A. lignicolus* were recorded and therefore a comparison of parasitoid richness with 2005 webs cannot be made. At Dunrobin, *T. auratus* and *S. umbraculus* emerged from *A. kollari* and, as at Beaully, only *T. auratus* emerged from *A. lignicolus*, which, as discussed previously, became established at this site since 1995. The same single inquiline species, *S. umbraculus*, was recorded from *A. kollari* at Dunrobin in both 1995 and 2005 (Table 4.2), however the parasitoid assemblage recorded from this gall differs from that recorded in 1995. In 1995, *A. kollari* was attacked by 3 parasitoid species (*E. brunneiventris*, *T. auratus*, and *C. fungosa*), only one of which was recorded from the gall in 2005 (*T. auratus*). One possible explanation for a decline in the number of parasitoid species recorded is the reduction in rearing sample size. In 1995, 280 *A. kollari* galls were reared at Dunrobin (Schönrogge *et al.*, 1999). In 2005, only 85 galls could be reared due to low gall density at the site (Table 4.1).

Since no invading asexual galls were recorded at Beaulieu in autumn 1995, no comparison can be made with attack rates from 2005. Attack rates for both *A. kollari* and *A. lignicolus* were very low for all parasitoid and inquiline species in 2005 (parasitoid density <1 per 100m² for most species) at both northern sites. Attack rates for *T. auratus* at Dunrobin in 2005 are one order of magnitude less than recorded in 1995 (Appendix, Table 7.3).

The quantitative webs from Beaulieu and Dunrobin do not indicate any significant changes in the interaction between parasitoid communities focused on native and invading gallwasps following the arrival of new invading species. In these northern webs, only one new invading species was recorded between 1995 and 2005 (*A. lignicolus* at Dunrobin).

4.3.4. Summaries from quantitative webs and linkage diagrams

A number of parameters taken from the quantified webs in Figures 4.1a-f illustrate the relationship between native and invading cynipid species at the 4 sites (Table 4.4). The number of species of cynipids, parasitoids, inquilines and links between gall species recorded in both spring and autumn generations were higher in the south than in the north, with twice as many gall-inducing cynipid species in southern as northern webs. More than twice as many parasitoids and inquiline species were recorded in southern webs compared with Beaulieu and over 3 times as many compared with Dunrobin (Tables 4.1 and 4.2). This is best illustrated by comparing the linkage diagrams for Silwood and Puttenham (Figures 4.2a,b,e,f) with the much simpler diagrams from Beaulieu and Dunrobin (Figures 4.2c,d).

Over both autumn and spring generations, native cynipid galls comprised 54% of all galls. However, separating spring and autumn generations, in spring 2005/6 invading species comprised 90% of all galls. In contrast, asexual generations of native cynipid

species were much more abundant than those of invading species, and comprised 99% of all recorded species.

The number of links between species was higher in spring than for autumn generations, notably in the south with the arrival of the invader *A. grossulariae*, which has numerous links with both native and alien cynipids. The linkage diagram for Silwood (Figure 4.2a) also shows the strong link between *A. grossulariae* and *A. quercuscalicis* galls, indicating that a large number of the parasitoids reared from *A. grossulariae* are also attacking *A. quercuscalicis*.

The number of shared inquiline and parasitoid species was higher for the southern webs with 6 species being shared at both Puttenham and Silwood in spring 2005. In contrast, only one incidence of shared parasitoids and inquilines was recorded from the northern webs, with one species (*M. fuscipes*) being shared at Dunrobin in spring 2005.

4.3.5. Potential for indirect interactions

Twenty species pairs of cynipid galls in autumn and spring (2005 and 2006) shared one or more parasitoid or inquiline species, as shown in Table 4.5. At Dunrobin, none of the spring galls shared any parasitoid or inquiline species with the autumn galls. Throughout all sites there was only one occasion where the spring and autumn galls of the same cynipid species, *A. quercuscalicis*, were attacked by the same parasitoid species, *C. fungosa*. This species attacked spring and autumn generations in 2005 and the spring generation of 2006 at Silwood.

Where parasitoid species were shared, most of the d_{ij} -values were < 0.1 (13 of 20 values) and two values were > 0.40 , indicating only weak indirect interactions. One exceptionally high value of 0.89 was recorded for the community shared between the spring galls of the invading cynipid *A. grossulariae* and the autumn galls of another

invader, *A. quercuscalicis* at Silwood. The parasitoid species that account for this interaction are *E. brunniventris*, *M. dorsalis*, *C. fungosa* and *E. urozonus*.

Table 4.1 Gall inducing cynipid species recorded at the 4 sites including sample sizes (*n*) reared for each generation. Sexual/Asexual gives the location of the galls of the corresponding generation of each species induced: B = bud, L = leaf, C = catkins, S = Stem, R = root, A = acorn. The superscript ^C indicates that these galls are exclusively formed on *Quercus cerris*. All other galls are formed on the native oak species *Q. robur* and/or *Q. petraea*. Invading cynipid species are printed in bold face. *Andricus aries* and *Aphelonyx cerricola* are currently known only from one generation.

CYNIPID SPECIES	Sexual	Asexual	Silwood		Puttenham		Beaulieu		Dunrobin	
			<i>n</i> sexuals	<i>n</i> asexuals	<i>n</i> sexuals	<i>n</i> asexuals	<i>n</i> sexuals	<i>n</i> asexuals	<i>n</i> sexuals	<i>n</i> asexuals
			2005/6	2005	2005/6	2005	2005	2005	2005	2005
<i>Andricus aries</i>		B	0	9	0	3	0	0	0	0
<i>Andricus corruptrix</i>	BC ^C	B	29/7	0	67/15	0	0	0	0	0
<i>Andricus curvator</i>	L	B/S	6/16	0	11/8	0	52	0	5	3
<i>Andricus fecundator</i>	C	B	0	8	0	1	0	0	0	0
<i>Andricus grossulariae</i>	C	A	150/150	14	150/150	0	0	0	0	0
<i>Andricus kollari</i>	BC ^C	B	150/150	26	150/150	0	60	150	150	85
<i>Andricus lignicolus</i>	BC ^C	B	150/150	80	150/150	0	150	150	150	22
<i>Andricus lucidus</i>	C ^C	B	0	1	0	1	0	0	0	0
<i>Andricus nudus</i>	C	B	0/1	0	0/4	0	0	0	0	0
<i>Andricus quadrilineatus</i>	C	B	4/0	0	0/150	0	83	4	8	42
<i>Andricus quercuscalicis</i>	C ^C	A	150/150	150	150/150	150	0	0	0	0
<i>Andricus solitarius</i>	C	B	6/0	0	0	0	0	0	0	0
<i>Aphelonyx cerricola</i>	BC ^C		5	0	0	0	0	0	0	0
<i>Biorhiza pallida</i>	B	R	0/150	0	0/150	0	27	0	0	0
<i>Cynips divisa</i>	B/L	L	1	9	0	10	1	150	0	18
<i>Cynips longiventris</i>	B	L	24/0	24	0	12	0	0	0	13
<i>Cynips quercusfolii</i>	B	L	0	150	0	67	0	0	0	0
<i>Neuroterus albipes</i>	L	L	1/0	150	0	150	0	14	0	0
<i>Neuroterus anthracinus</i>	B	L	0	150	0	150	0	0	0	0
<i>Neuroterus numismalis</i>	L	L	22/0	1000	150/0	1000	0	1000	0	16
<i>Neuroterus quercusbaccarum</i>	L	L	77/0	1000	150/0	1000	12	1000	83	40
SPECIES RICHNESS			21		19		9		8	

Table 4.2 Parasitoid and inquiline (Synergus) species recorded from the 4 sample sites from spring 2005 to spring 2006.

Parasitoid family	Silwood	Puttenham	Beaulieu	Dunrobin
Torymidae	<i>Megastigmus dorsalis</i> <i>Megastigmus stigmatizans</i> <i>Torymus flavipes</i>	<i>M. dorsalis</i> <i>T. flavipes</i> <i>Torymus geranii</i> <i>Torymus auratus</i>	<i>T. auratus</i> <i>T. flavipes</i> <i>T. geranii</i> <i>Torymus cerri</i> <i>Torymus affinis</i> <i>Torymus spp</i>	<i>T. auratus</i> <i>T. flavipes</i>
Ormyridae	<i>Ormyrus nitidulus</i> <i>Ormyrus sp.</i>	<i>O. nitidulus</i>		
Eurytomidae	<i>Eurytoma brunniventris</i> <i>Sycophila biguttata</i>	<i>E. brunniventris</i> <i>S. biguttata</i> <i>Sycophila variagata</i>		
Pteromalidae	<i>Mesopolobus sericeus</i> <i>Mesopolobus fuscipes</i> <i>Mesopolobus tibialis</i> <i>Mesopolobus xanthocerus</i> <i>Mesopolobus amaenus</i> <i>Mesopolobus dubius</i> <i>Mesopolobus fasciiventris</i> <i>Ormocerus vernalis</i> <i>Cecidostiba fungosa</i> <i>Eupelmus urozonus</i>	<i>M. fuscipes</i> <i>M. tibialis</i> <i>M. amaenus</i> <i>M. xanthocerus</i> <i>M. dubius</i> <i>M. sericeus</i> <i>Mesopolobus fasciiventris</i> <i>C. fungosa</i> <i>Cecidostiba semifascia</i> <i>E. urozonus</i>	<i>M. fuscipes</i>	<i>M. fuscipes</i> <i>M. dubius</i> <i>M. tibialis</i>
Eupelmidae Eulophidae	<i>Pediobius sp.</i>	<i>Aulogymnus skianeuros</i>	<i>A. skianeuros</i>	
Synergus spp.	<i>S. radiatus/pallipes</i> <i>S. gallaepomiformis</i> <i>S. pallidipennis</i> <i>Synergus sp.</i>	<i>S. radiatus/pallipes</i> <i>S. gallaepomiformis</i> <i>S. pallidipennis</i> <i>S. umbraculus</i>	<i>S. umbraculus</i>	<i>S. umbraculus</i>
Species richness	22	23	9	6

Table 4.3 Abundance of gall inducing cynipid species at each of the 4 sites in spring 2005, autumn 2005 and spring 2006. Some species, although present at the sites, were below detectable densities during random sampling (-). Some species were not recorded at particular sites (n/a). Invading cynipid species are printed in bold

Silwood 2005	Galls/100m ²	Silwood 2005	Galls/100m ²
Spring		Autumn	
Andricus quercuscalicis	23697.56	<i>N. quercusbaccarum</i>	9891.45
Andricus grossulariae	5491.21	<i>N. numismalis</i>	1119.57
<i>N. quercusbaccarum</i>	4547.19	<i>N. anthracinus</i>	883.73
Andricus lignicolus	2205.76	<i>N. albipes</i>	493.52
<i>Neuroterus numismalis</i>	766.53	<i>C. longiventris</i>	38.64
Andricus corruptrix	159.62	A. quercuscalicis	35.44
Andricus kollari	75.25	<i>C. divisa</i>	5.77
<i>Andricus solitarius</i>	52.02	<i>A. aries</i>	-
<i>Andricus curvator</i>	6.21	<i>A. kollari</i>	-
Andricus lucidus	-	A. corruptrix	-
		A. lignicolus	-
		A. lucidus	-
<hr/>			
Puttenham 2005	Galls/100m ²	Puttenham 2005	Galls/100m ²
Spring		Autumn	
A. quercuscalicis	23936.56	<i>N. quercusbaccarum</i>	21726.72
A. lignicolus	8752.32	<i>N. albipes</i>	8941.22
A. corruptrix	6547.26	<i>N. anthracinus</i>	1047.59
A. grossulariae	3964.79	A. aries	421.99
<i>N. quercusbaccarum</i>	3904.38	A. quercuscalicis	306.23
A. kollari	1942.34	<i>N. numismalis</i>	35.78
<i>N. numismalis</i>	1087.09	<i>A. fecundator</i>	24.06
<i>A. curvator</i>	409.29	A. kollari	-
A. lucidus	-	A. cerricola	n/a
		A. corruptrix	-
		A. lignicolus	-
		A. lucidus	-
<hr/>			
Beaully 2005	Galls/100m ²	Beaully 2005	Galls/100m ²
Spring		Autumn	
<i>A. quadrilineatus</i>	1400.01	<i>N. quercusbaccarum</i>	46412.95
A. lignicolus	537.36	<i>N. numismalis</i>	176.05
<i>N. quercusbaccarum</i>	153.00	A. lignicolus	102.18
<i>B. pallida</i>	125.60	A. kollari	94.92
A. kollari	30.95	<i>N. albipes</i>	72.67
A. quercuscalicis	n/a	<i>C. divisa</i>	63.41
A. grossulariae	n/a	A. quercuscalicis	n/a
A. corruptrix	n/a	A. corruptrix	n/a
A. lucidus	n/a	A. cerricola	n/a
		A. lucidus	n/a
		A. aries	n/a

Table 4.3 (Continued)

Dunrobin 2005	Galls/100m ²	Dunrobin 2005	Galls/100m ²
Spring		Autumn	
A. lignicolus	135.95	<i>N. quercusbaccarum</i>	7.13
A. kollari	117.20	<i>N. numismalis</i>	2.40
<i>N. quercusbaccarum</i>	23.72	<i>A. kollari</i>	0.63
<i>A. quadrilineatus</i>	7.73	A. lignicolus	0.47
<i>A. curvator</i>	3.06	<i>C. longiventris</i>	0.32
A. quercuscalicis	n/a	A. quercuscalicis	n/a
A. grossulariae	n/a	A. corruptrix	n/a
A. corruptrix	n/a	<i>A. aries</i>	n/a
Andricus lucidus	n/a	A. cerricola	n/a
		A. lucidus	n/a
Rearings for Spring 2006			
Silwood 2006	Galls/100m ²	Puttenham 2006	Galls/100m ²
Spring		Spring	
A. quercuscalicis	2463.32	A. quercuscalicis	26743.30
A. lignicolus	603.22	A. lignicolus	10666.50
<i>B. pallida</i>	392.81	A. grossulariae	8303.18
<i>A. curvator</i>	339.50	A. corruptrix	758.48
A. grossulariae	288.63	<i>B. pallida</i>	376.08
<i>N. quercusbaccarum</i>	94.53	<i>A. curvator</i>	66.67
A. corruptrix	53.05	A. kollari	50.95
A. kollari	21.23	<i>A. nudus</i>	5.95
A. lucidus	-		

Table 4.4 Summaries of parameters taken from quantitative webs. Generations have been split into spring and autumn to allow comparisons

Generations	Spring 2005				Autumn 2005				Spring 2006	
	Silwood	Puttenham	Beaulieu	Dunrobin	Silwood	Puttenham	Beaulieu	Dunrobin	Silwood	Puttenham
No. of species	24	25	8	8	14	9	7	4	27	22
No. of links	31	33	8	7	12	8	6	3	29	24
Σ Natives	4560	4991	278	27	922	1048	0	0	393	376
Σ Aliens	31629	43201	0	256	35	306	197	0	3429	11428
% Aliens	87	90	0	91	4	23	100	100	90	97
Li/native sp	10.3	11	4	3.5	6	9	0	0	1	24
Li/alien sp.	6.2	8.3	0	3.5	12	9	3	1.5	5.8	8
Links/species ²	0.48	0.67	0.125	0.11	0.06	0.01	0.12	0.19	0.04	0.05
P. sp.	13	15	5	4	9	5	4	1	20	17
I. sp.	3	3	1	0	2	2	1	1	1	1
Li/P + I. sp	1.83	1.83	1.33	1.75	1.09	1.29	1.2	1.5	1.38	1.33
P. + I. sp. att. alien sp.	14	13	0	1	10	6	5	2	8	7
P. +I. sp. shared between Natives and aliens	6	6	0	1	1	1	0	0	4	5
Σ P. + I. from aliens	27297	27909	0	13	3	295	39	1	485	1012
Σ P. + I. from natives	4878	5401	198	19	899	1047	0	0	81	67

Li = Links; P. + I. sp. = parasitoid and inquiline species; aliens = number of invading species present at the site above detectable densities; natives = number of native species present at that site; Σ = number of individuals/100m².

Table 4.5 D_j -values for the indirect interactions among local gall inducing cynipid populations between generations. The table includes only the galls of those cynipid species where at least share at least one parasitoid or inquiline species was shared. No parasitoid or inquiline species was shared between the autumn and spring galls collected at Dunrobin. Invading species are printed in bold.

Site	Spring galls	Autumn galls		
Silwood (spring/autumn 2005)	<i>A. curvator</i>	<i>C. longiventris</i>	<i>A. quercuscalicis</i>	<i>N. anthracinus</i>
	<i>A. grossulariae</i>	0.3000	0.8910	
	<i>N. quercusbaccarum</i>	0.0554	0.0420	0.0317
Puttenham (spring/autumn 2005)		<i>A. quercuscalicis</i>	<i>N. anthracinus</i>	
	<i>A. quercuscalicis</i>	0.0046		
	<i>N. quercusbaccarum</i>	0.4237	0.4783	
	<i>N. numismalis</i>	0.0003		
Beaully (spring/autumn 2005)	<i>A. grossulariae</i>	0.0200	0.0121	
		<i>A. kollari</i>		
	<i>N. quercusbaccarum</i>	0.0070		
Silwood (autumn 2005/spring 2006)	<i>B. pallida</i>	0.0007		
		<i>A. quercuscalicis</i>	<i>N. anthracinus</i>	
	<i>B. pallida</i>	0.0480	0.1050	
	<i>A. quercuscalicis</i>	0.0010		
Puttenham (autumn 2005/spring 2006)	<i>A. grossulariae</i>	0.0010		
		<i>A. quercuscalicis</i>		
	<i>B. pallida</i>	0.2208		
		0.2807		

Figure 4.1a Quantitative web for Silwood, spring/autumn 2005. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *A. corruptrix*(S), *A. grossulariae*(S), *A. kollari*(S), *A. lignicolus*(S), *A. quercuscalicis*(S), *A. curator*(S), *N. numismalis*(S), *N. quercusbaccarum*(S), *A. quercuscalicis* (A), *C. longiventris*(A), *N. anthracinus*(A). The conventions used in drawing the webs are fully explained in the text.

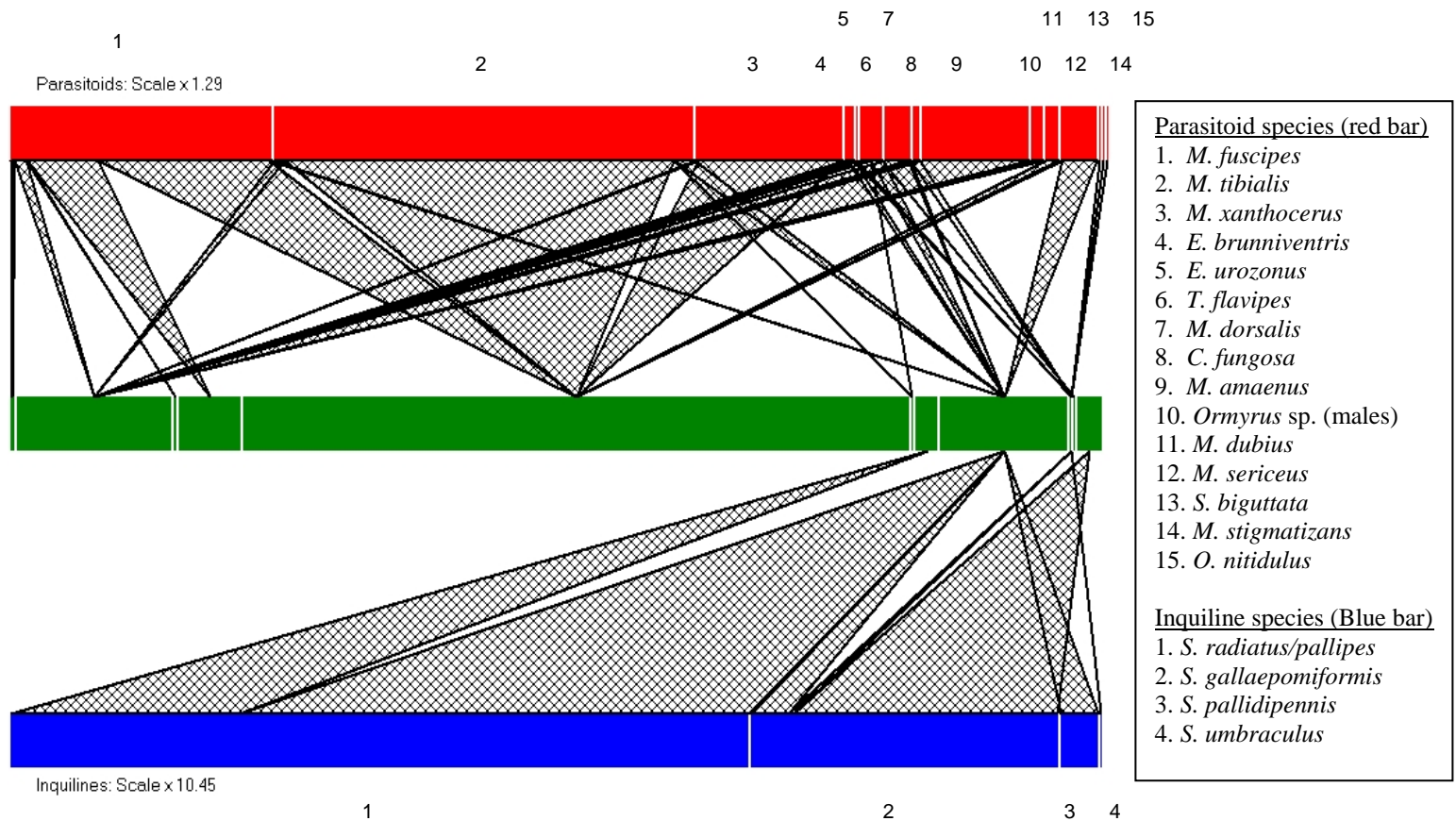


Figure 4.1b Quantitative web for Puttenham, spring/autumn 2005. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *A. corruptrix* (S), *A. grossulariae* (S), *A. lignicolus* (S), *A. quercuscalicis* (S), *A. curvator* (S), *N. numismalis* (S), *N. quercusbaccarum* (S), *A. quercuscalicis* (A), *N. anthricinus* (A).

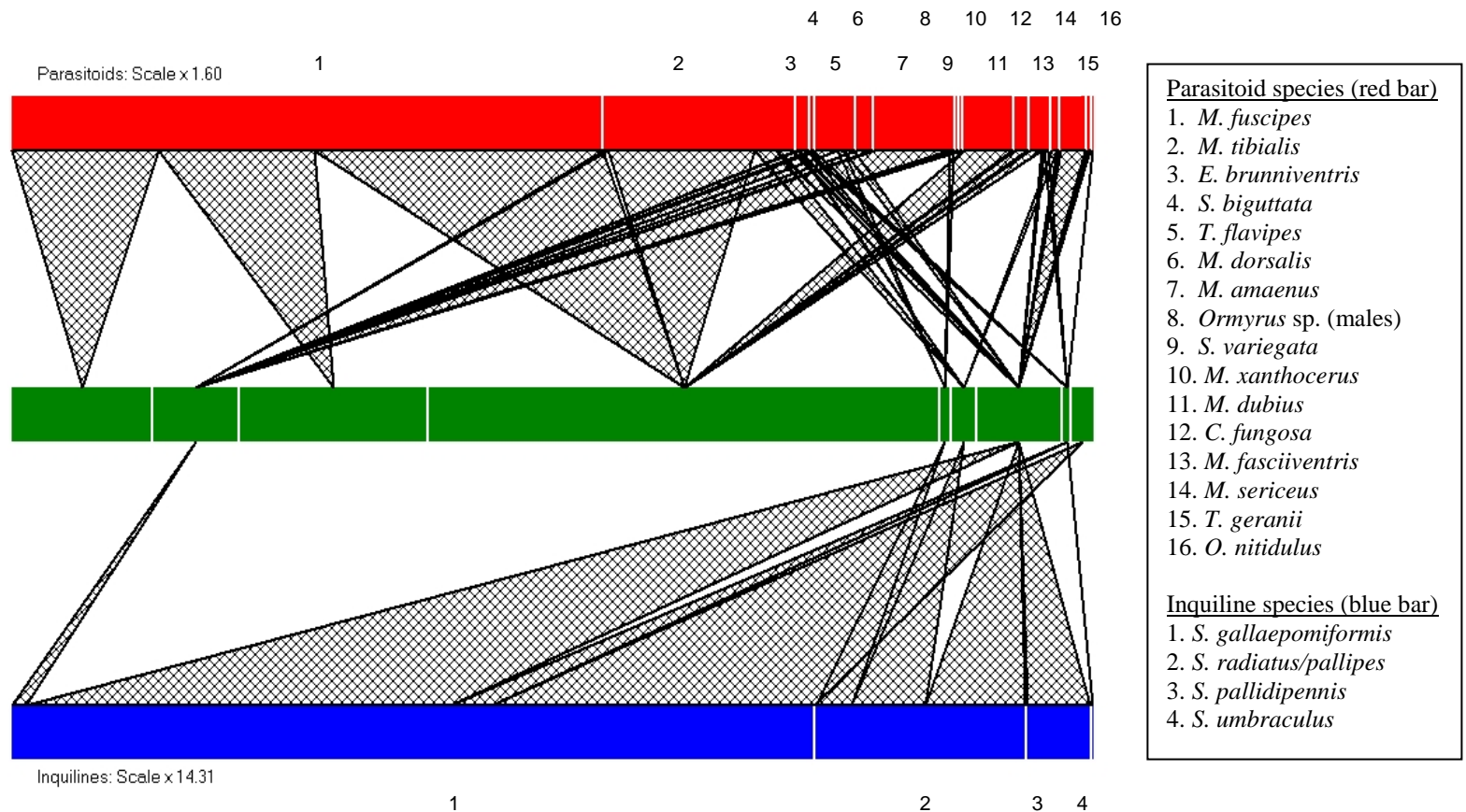


Figure 4.1c Quantitative web for Beauly, spring/autumn 2005. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *B. pallida*(S), *N. quercusbaccarum*(S), *A. kollari*(A), *A. lignicolus*(A).

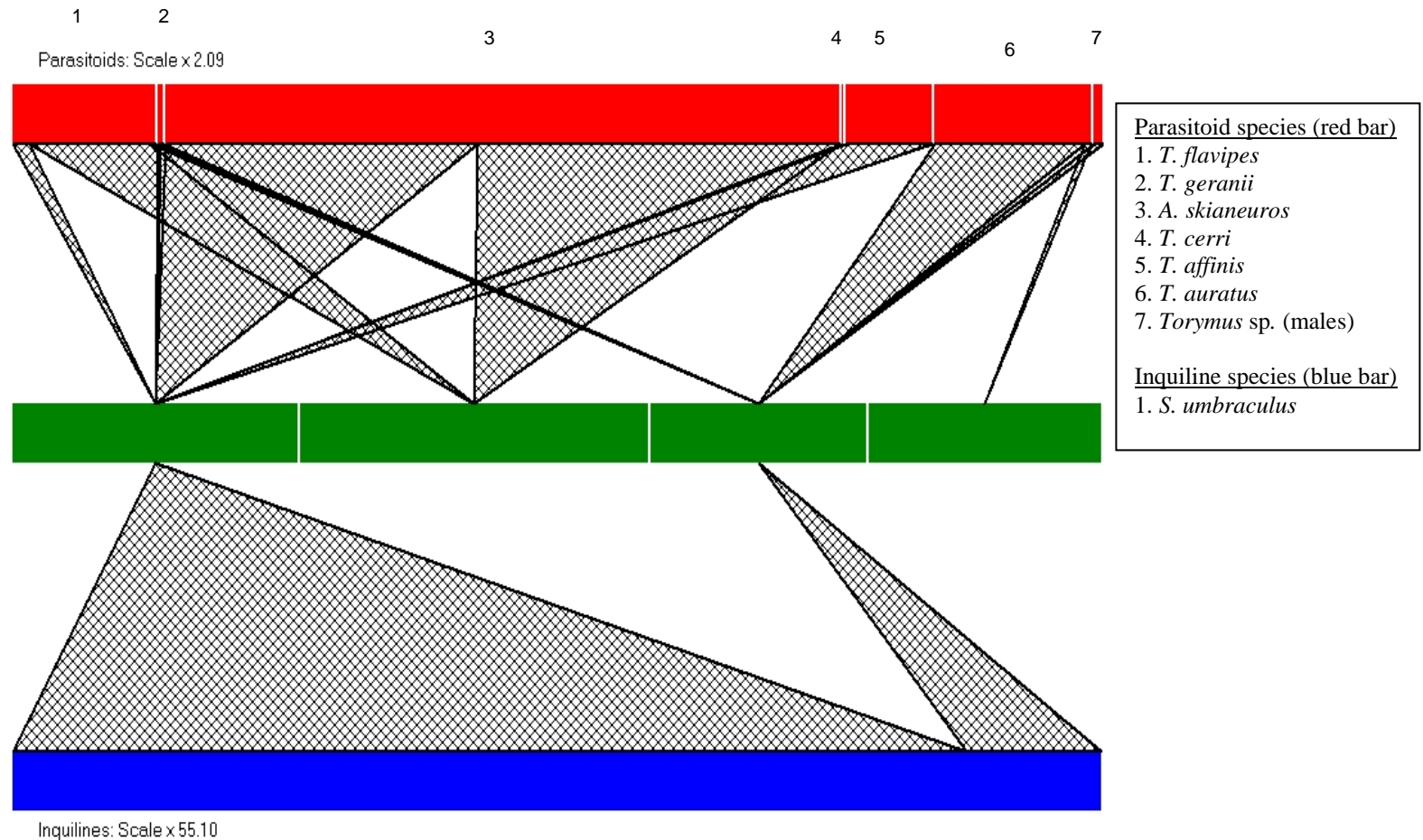


Figure 4.1d Quantitative web for Dunrobin, spring/autumn 2005. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *A. kollari*(S), *A. lignicolus*(S), *A. curvator*(S), *N. quercusbaccarum*(S), *A. kollari*(A), *A. lignicolus*(A).

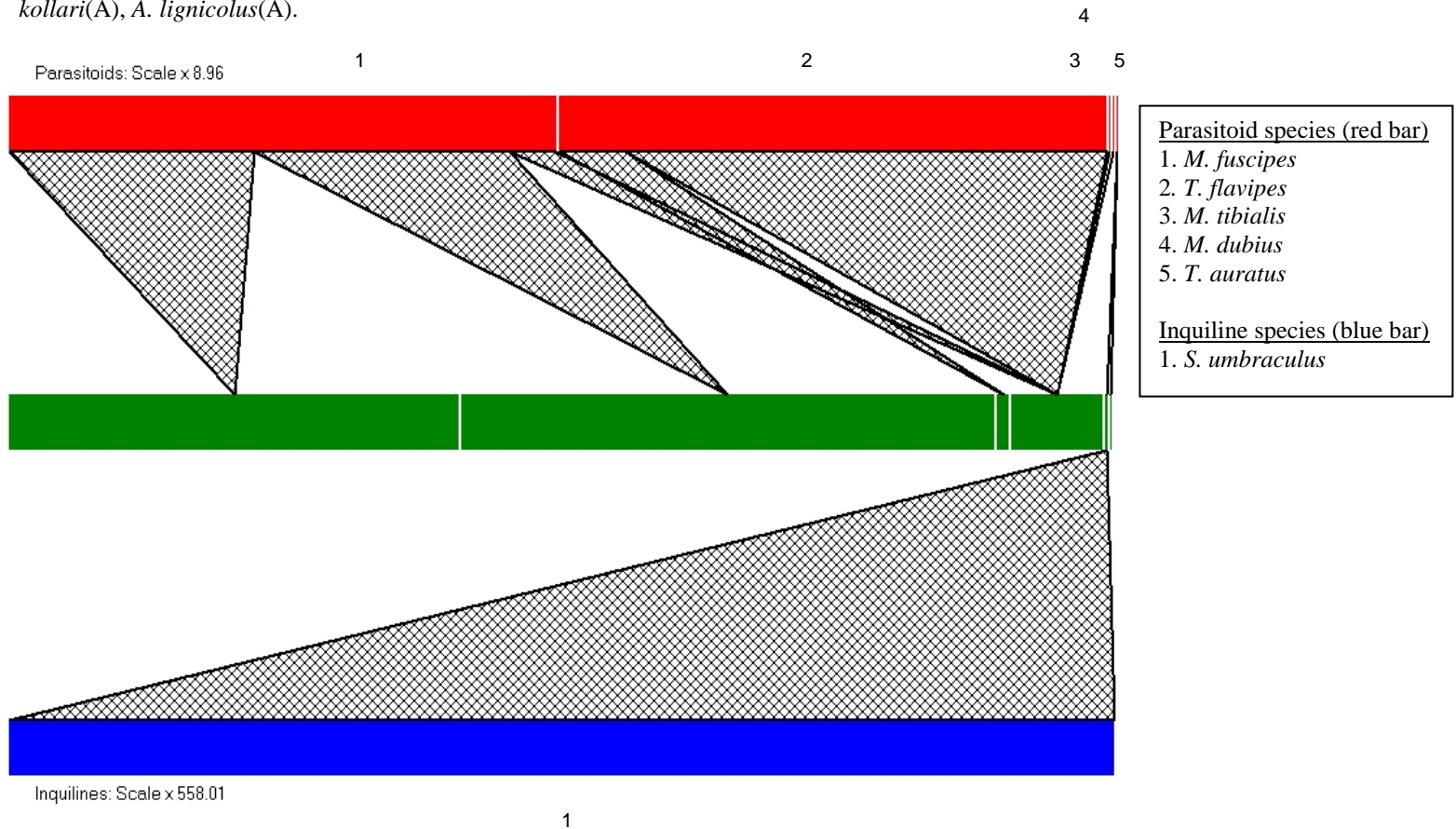


Figure 4.1e Quantitative web for Silwood, autumn 2005/spring 2006. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *A. quercuscalicis*(A), *C. longiventris*(A), *N. anthracinus*(A), *A. corruptrix*(S), *A. kollari*(S), *A. lignicolus*(S), *A. grossulariae*(S), *A. quercuscalicis*(S), *B. pallida*(S).

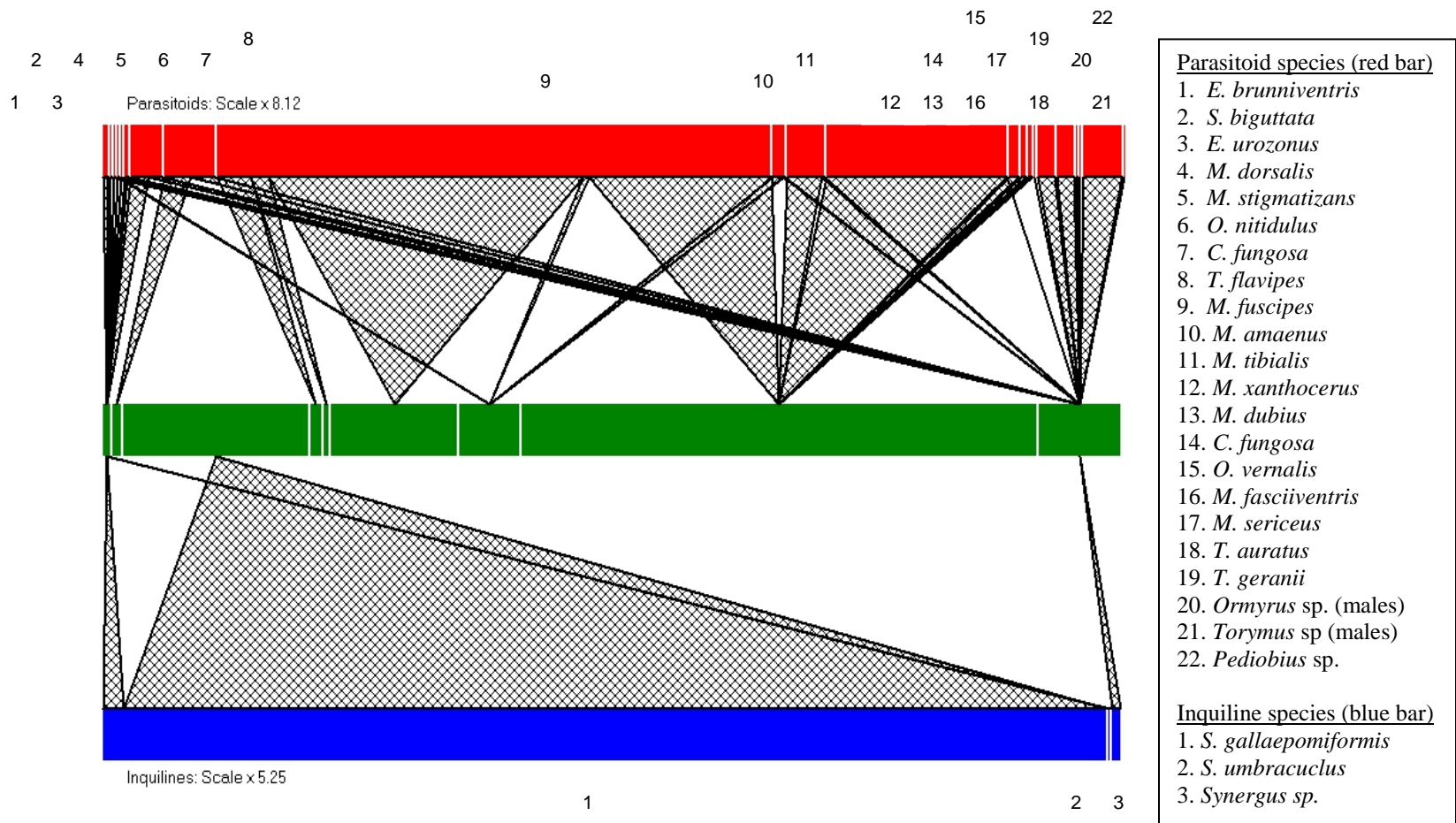


Figure 4.1f Quantitative web for Puttenham, autumn 2005/spring 2006. Cynipid gall species are represented by the green central bar. Gall inducer species from left to right (S = sexual generation; A = asexual generation): *A. quercuscalicis*(A), *N. anthracinus*(A), *A. corruptrix*(S), *A. grossulariae*(S), *A. lignicolus*(S), *A. quercuscalicis*(S), *B. pallida*(S).

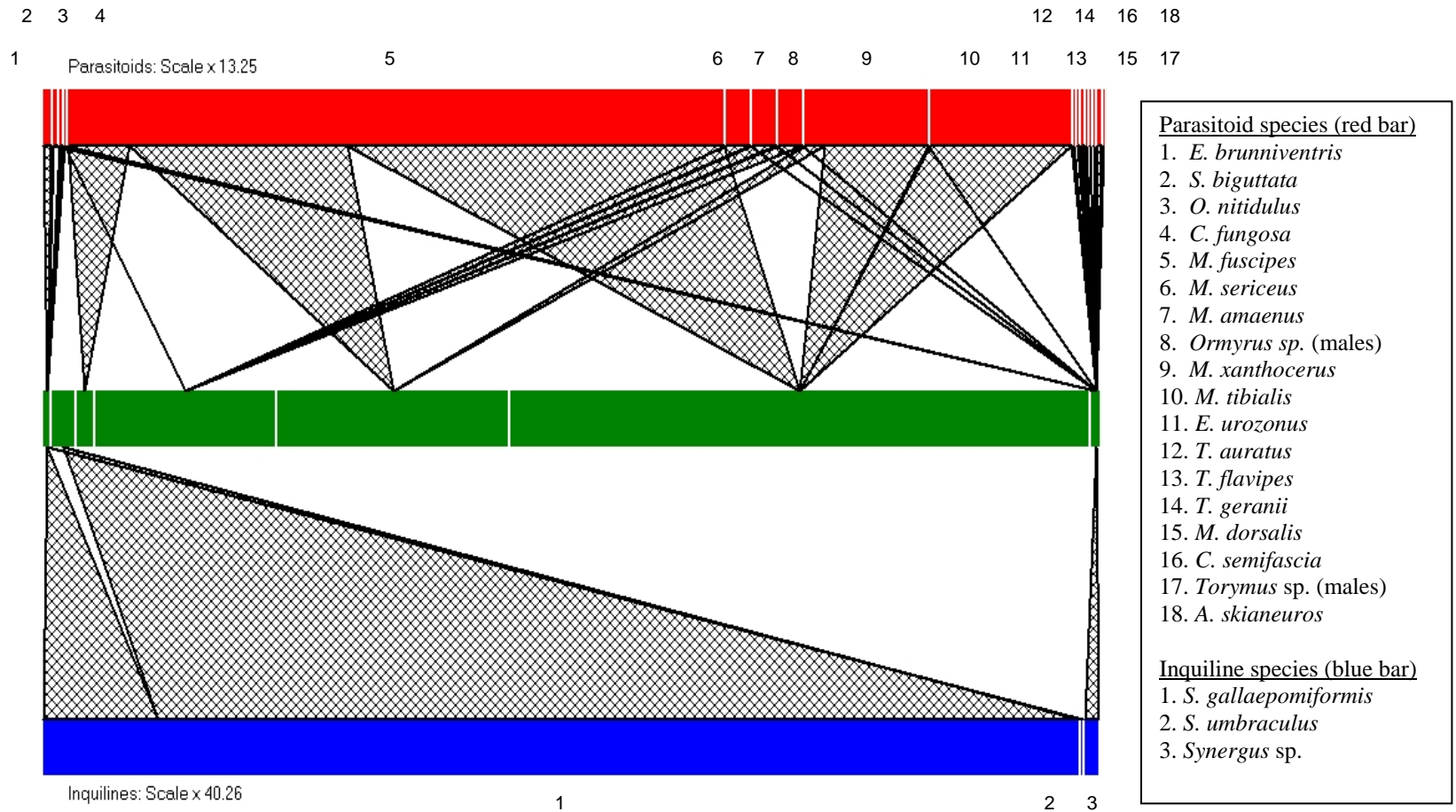


Figure 4.2a Cynipid communities and their links via shared parasitoids illustrated as social networks for Silwood, spring/autumn 2005. The conventions used in drawing the linkage diagrams are fully explained in the text. Gall species listed in the column on the left have symbols scaled by their relative abundance, but produced no parasitoids.

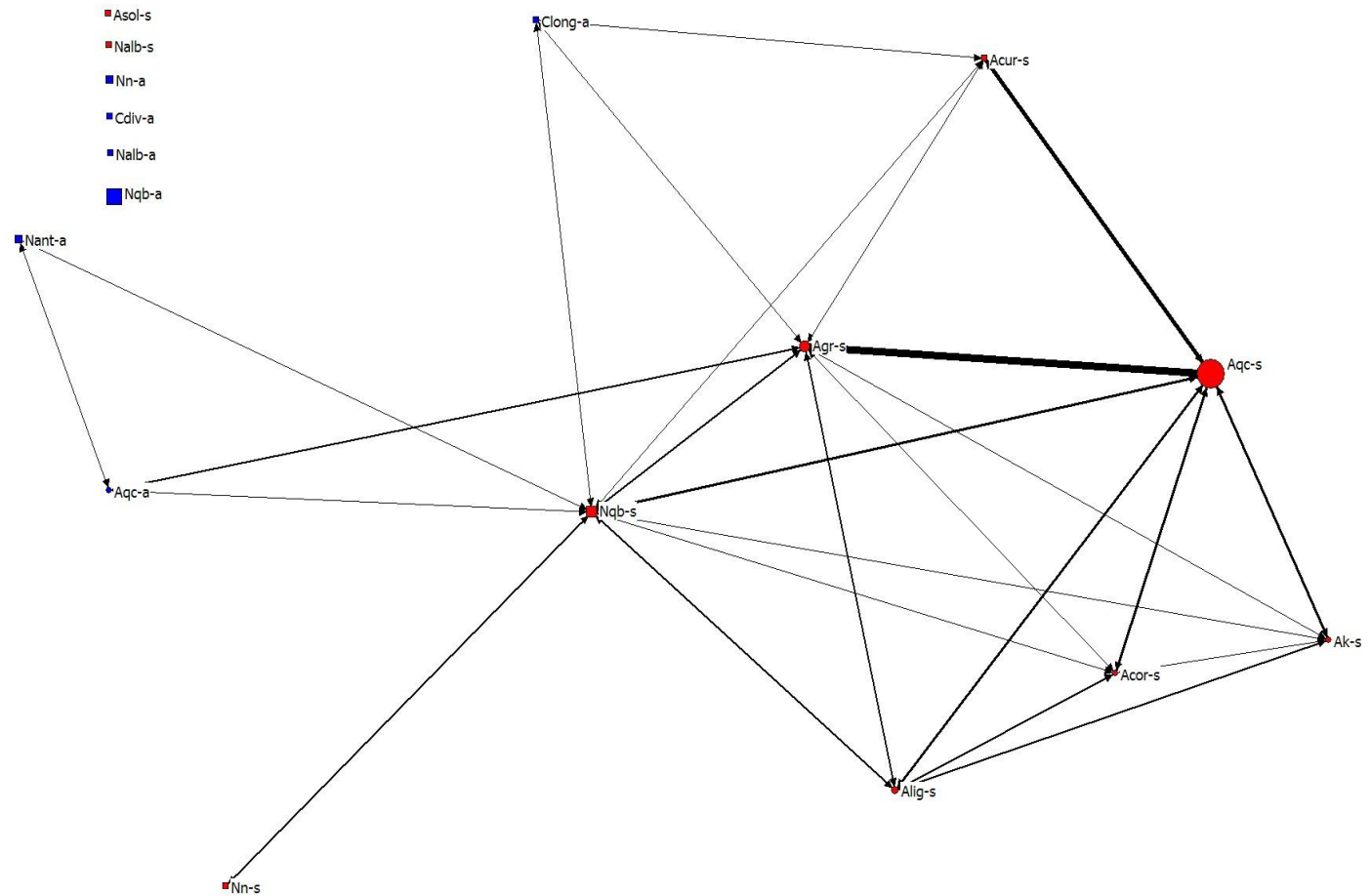


Figure 4.2b Cynipid communities and their links via shared parasitoids illustrated as social networks for Puttenham, spring/autumn 2005. Gall species listed in column on the left have symbols scaled by their relative abundance, but produced no parasitoids.

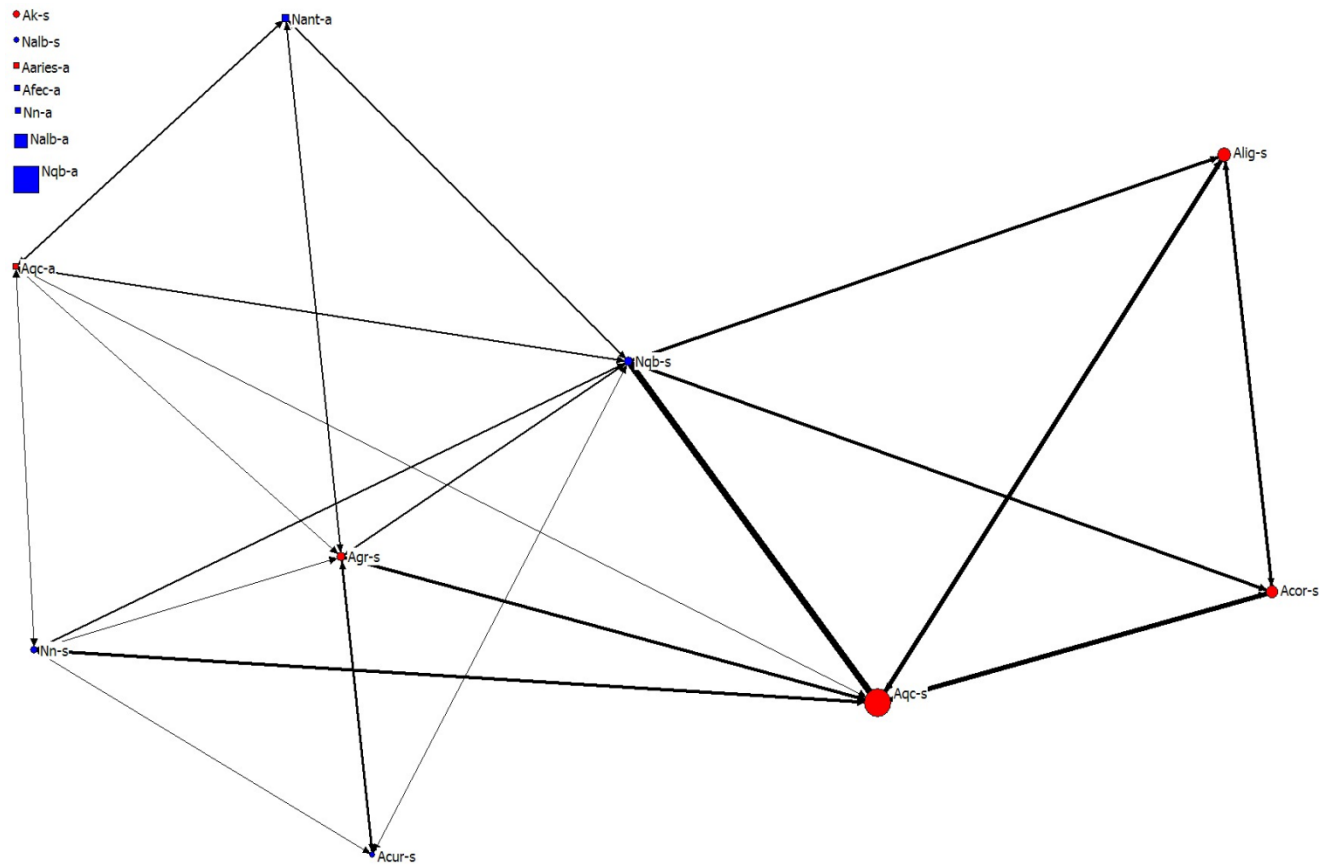


Figure 4.2c Cynipid communities and their links via shared parasitoids illustrated as social networks for Beauy, spring/autumn 2005. Gall species listed in column on the left have symbols scaled by their relative abundance, but produced no parasitoids.

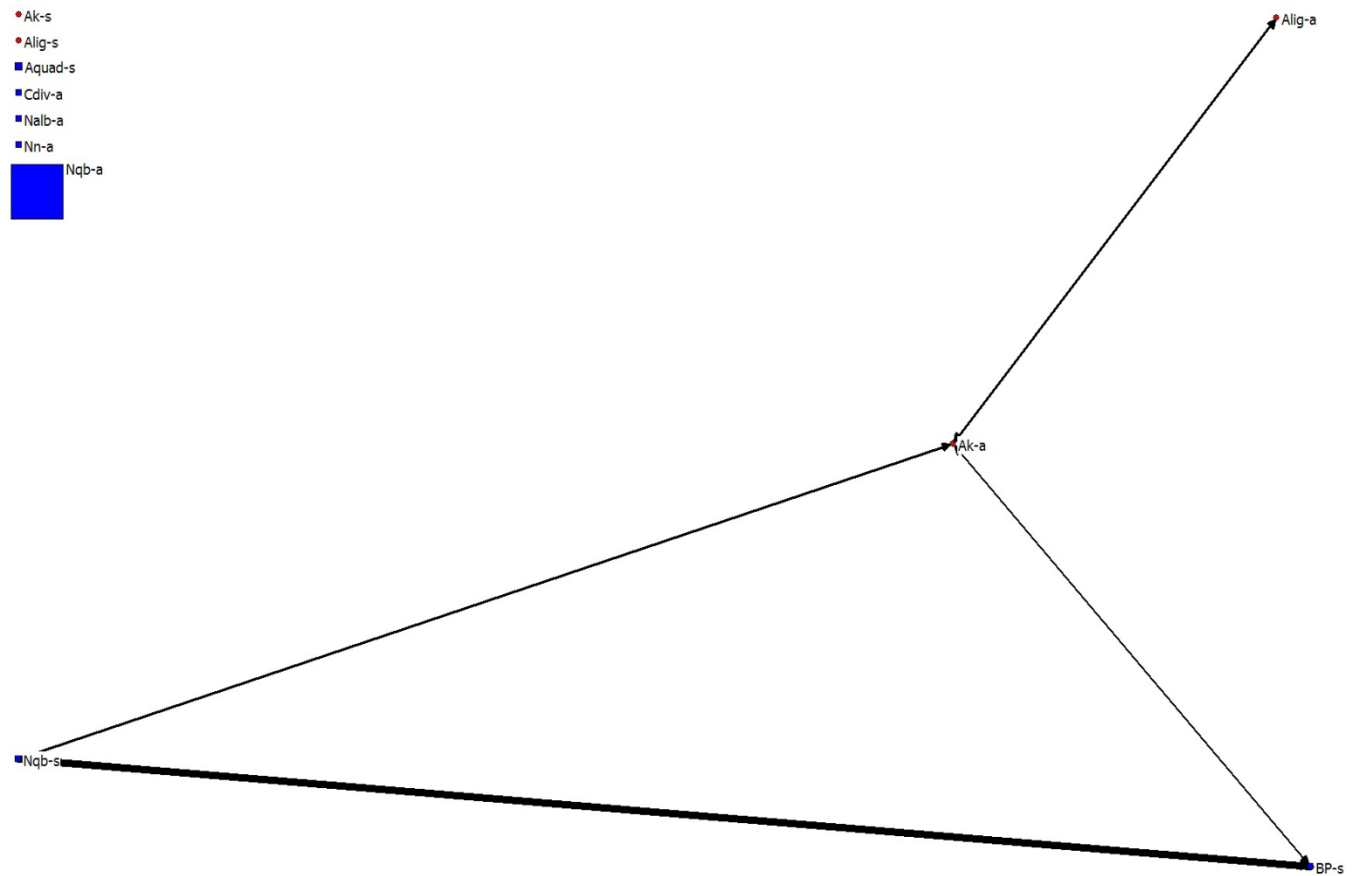


Figure 4.2d Cynipid communities and their links via shared parasitoids illustrated as social networks for Dunrobin, spring/autumn 2005. Gall species listed in column on the left have symbols scaled by their relative abundance, but produced no parasitoids.

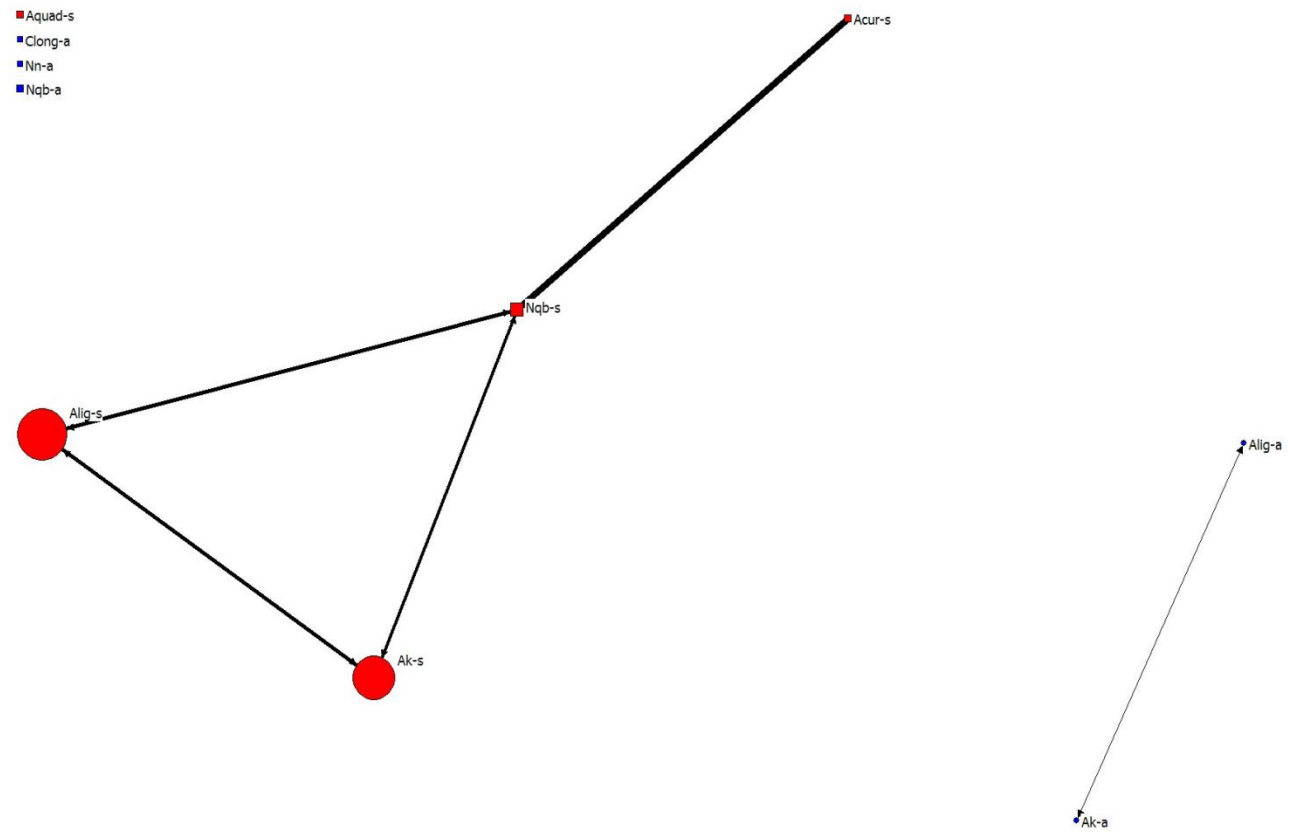


Figure 4.2e Cynipid communities and their links via shared parasitoids illustrated as social networks for Silwood, autumn 2005/spring 2006. Gall species listed in column on the left have symbols scaled by their relative abundance, but produced no parasitoids.

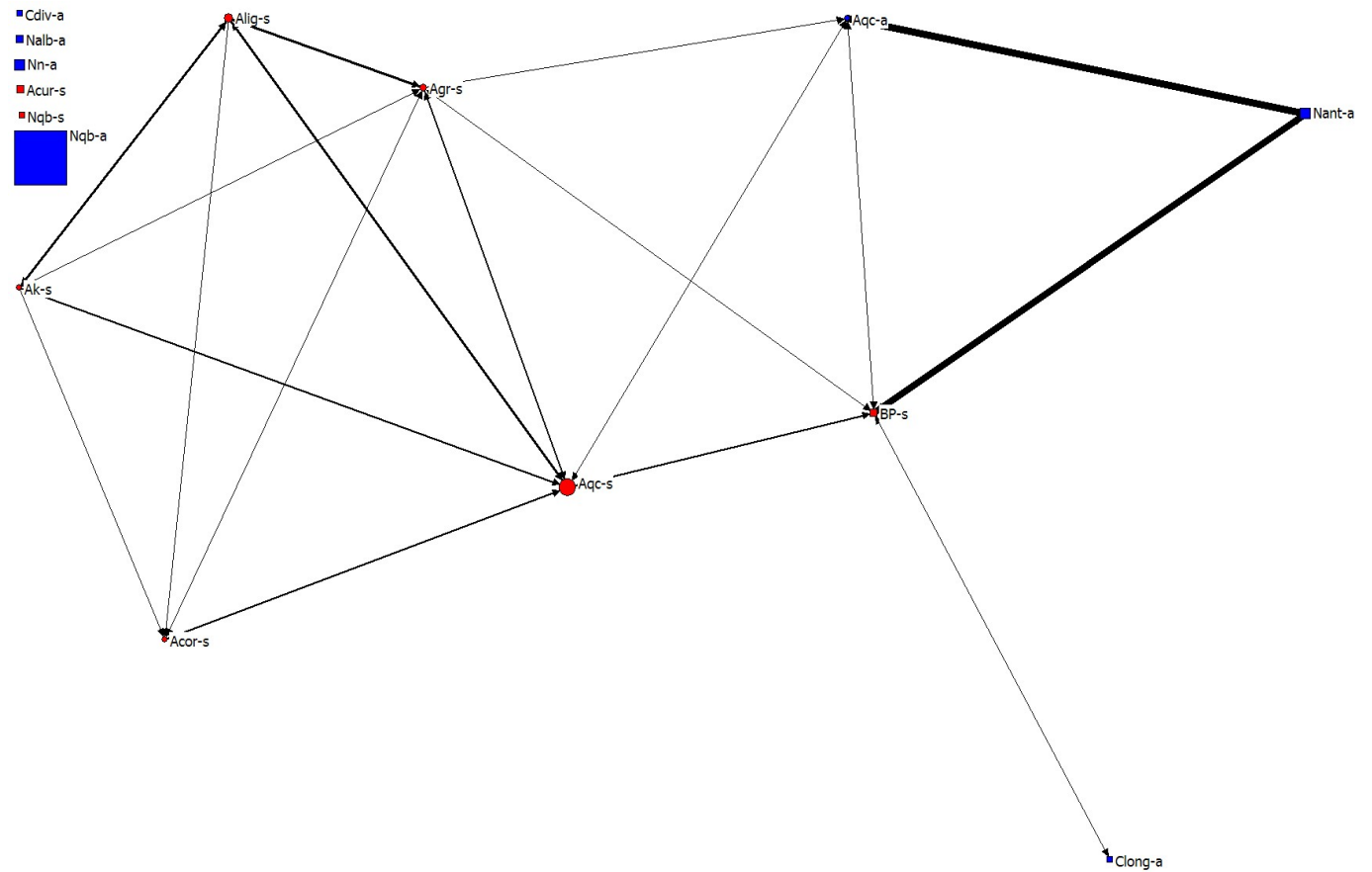
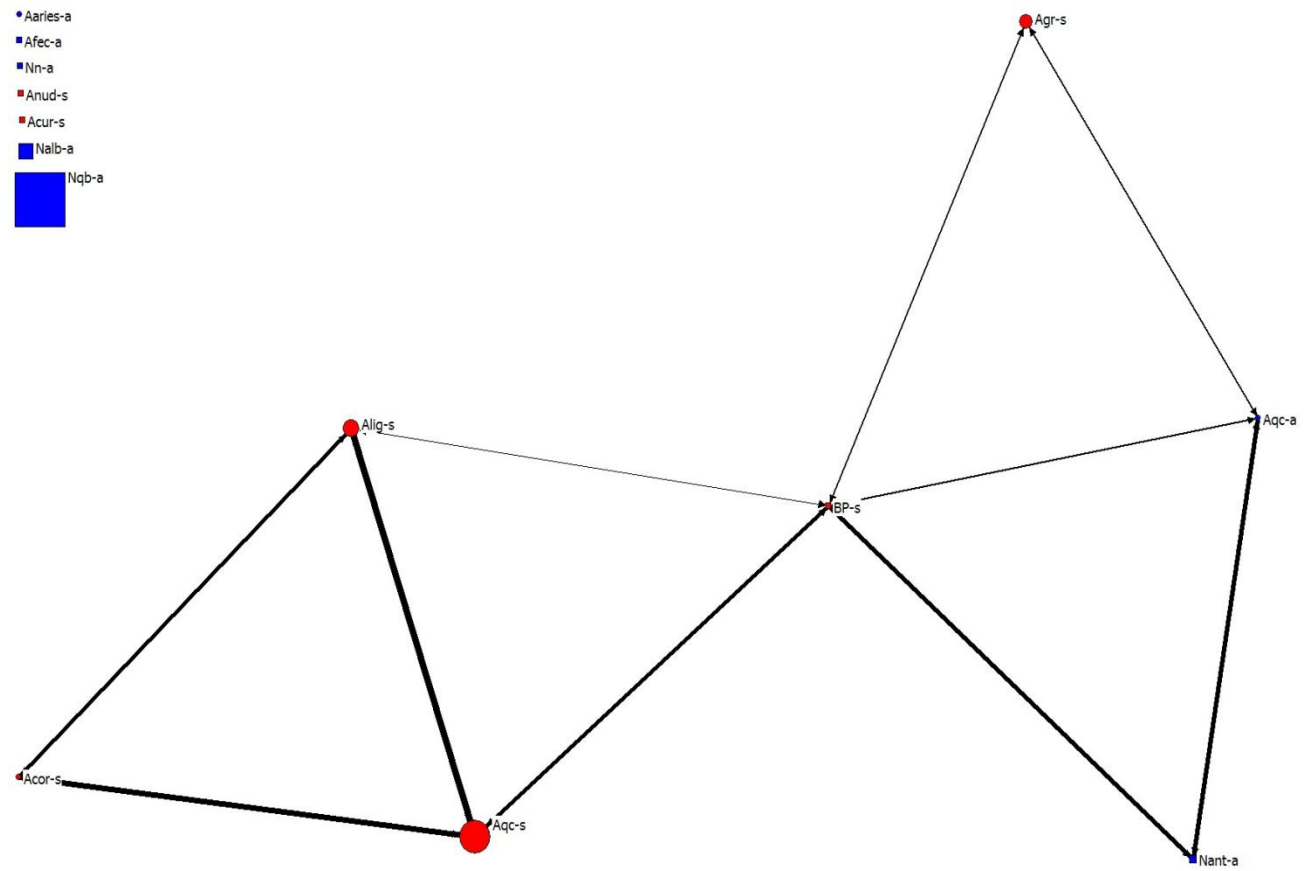


Figure 4.2f Cynipid communities and their links via shared parasitoids illustrated as social networks for Puttenham, autumn 2005/spring 2006. Gall species listed in column on the left have symbols scaled by their relative abundance, but produced no parasitoids.



4.4 Discussion

The arrival of 4 more invading cynipid species in the south of Britain has resulted in significant differences between quantitative webs for sites in northern Scotland and southern England, with fewer trophic links between species in quantitative webs in the north.

The new invaders that have sexual generations on *Q. cerris* have rapidly formed trophic links via shared parasitoids with the sexual generations of the first set of invaders that are found on the same host (*Q. cerris*). In southern Britain, *A. grossulariae* shares at least one parasitoid species, *Mesopolobus fuscipes*, found in the parasitoid assemblages associated with each of the 4 established invading cynipids (*A. quercuscalicis*, *A. corruptrix*, *A. kollari* and *A. lignicolus*). In the case of *A. grossulariae* and *A. quercuscalicis*, three parasitoid species are shared.

However, in contrast to previous studies, newly arriving gallwasp generations do not fall wholly within trophic compartments based on their host oaks (Schönrogge and Crawley, 2000). Importantly, the arrival *A. grossulariae* has linked communities associated with galls on *Q. petraea/robur* and *Q. cerris*, breaking down the previously observed compartmentalisation of the sexual generation galls on these two oak hosts. The arrival of *A. grossulariae* in southern Britain has also increased the number and complexity of links between cynipid galls via shared parasitoids.

Recent studies have demonstrated that fully quantitative webs are a useful way of investigating aspects of community structure and function and importantly, are essential to assess the importance of indirect interactions such as apparent competition (Memmott and Godfray, 1994; Memmott *et al.*, 1994; Müller *et al.*, 1999; Schönrogge and Crawley, 2000; Rott and Godfray, 2000; Valladares *et al.*, 2001; Lewis *et al.*, 2002; Wills and Memmott, 2005; Montoya *et al.*, 2006). Using quantitative webs as a tool to examine community structure is, however, not without problems and there are potential sources

of bias alluded to by several authors (Müller *et al.*, 1999; Rott and Godfray, 2000; Valladares *et al.*, 2001; van Veen *et al.*, 2006). Importantly, biases that relate specifically to webs constructed for cynipid communities are described in Schönrogge and Crawley (2000). These biases are discussed in my concluding chapter (Chapter 6) together with a section suggesting future work in relation to the use of quantitative webs.

In this study, quantitative webs and linkage diagrams allow comparisons between UK cynipid communities before and after recent invasion of 4 alien cynipid wasp species (*A. aries*, *A. lucidus*, *A. grossulariae* and *Aphelonyx cerricola*) in Britain. The decade between 1995 and 2005 has seen significant changes in cynipid communities, both at the southern sites at Silwood and Puttenham, and the northern sites at Beauly and Dunrobin.

Parasitoid recruitment to invading cynipid galls in Britain is continuing in the south of Britain, where 8 new invading cynipid species have arrived over the last 10 years. For the three *Plagiotrochus* species and *Neuroterus saliens*, only the first records of the occurrence are published and their status in terms of parasitoid recruitment is unknown (Hancy and Hancy, 2004; Redfern, 2006; Robbins, 2007). For the species that have been known for a number of years, including *A. lucidus*, *A. aries*, and *Aphelonyx cerricola*, there are also no published parasitoid records for Britain. However, *A. grossulariae* has spread and populations both at Silwood and Puttenham have increased tremendously. Addition of this species has affected the community structure significantly, particularly by linking galls on *Q. cerris* to those on native oaks via shared parasitoid species. If and when the other alien species recruit natural enemies, one would expect these communities to increase in complexity, e.g. increased linkage densities (Dunne *et al.*, 2002). However, where species pairs are vulnerable to apparent competition, as indicated by the high D_{ij} value between *A. quercuscalicis* and *A. grossulariae*, the outcome could lead to the replacement of a resident species or the prevention of the long term establishment of the new alien (Washburn and Cornell, 1981; Holt and Lawton, 1994; Morris *et al.*, 2004).

Also, differences in parasitoid species composition have been detected. At both Silwood and Puttenham, one additional species has been recorded adding to the parasitoid species pool at both sites. At Silwood, the torymid *Megastigmus stigmatizans* was recorded for the first time. This large parasitoid attacks asexual generations of *A. quercuscalicis* and has previously been recorded in south west England where it was reared from *A. kollari* asexual galls. At Puttenham, *M. sericeus* was recorded from the sexual spring gall of *A. grossulariae*. In the sexual spring generation galls at both southern sites there has been a large increase in the richness of parasitoids attacking invading cynipids. This is due to the large contribution of parasitoid richness made by the arrival of *A. grossulariae*, which has the most diverse parasitoid assemblage of any of the invading cynipids in spring. *A. grossulariae* was first recorded in Britain in 2001 (Walker, 2001).

At the northern sites, there has been no additional recruitment to parasitoid assemblages of individual gall species. The community richness of parasitoid and inquiline species recorded from cynipid galls has declined, largely due to low density of native cynipids, a factor which could reduce the pool of parasitoids available to attack invading species, however, it must be considered that these statements are extrapolations from random sampling of the cynipid community.

Despite the arrival of new invading cynipid species in the south of Britain and range expansion to the northern sites of Dunrobin by *A. lignicolus*, a decline in cynipid species richness has occurred at all 4 sites over the last 10 years. This decline can be attributed to the decrease in the number of native cynipid species recorded which in 2005/6 was around half that recorded in 1994/5 at each of the 4 sites (Schönrogge & Crawley 2000). Cynipid densities can fluctuate greatly from year to year (Schönrogge *et al.*, 1999; Schönrogge and Crawley, 2000). In this study, *B. pallida* was rare at the southern sites in spring 2005, yet abundant at the same sites in spring 2006, increasing by a factor of 10 on the sampled trees and was observed to be even more abundant on other trees at the same sites. Conversely, *N. quercusbaccarum* featured in the communities in the south in spring 2005 but only a few individuals were recorded in spring 2006. There is also

some evidence from long term datasets to suggest that over the last few decades there has been a general decline in the density of some species of native cynipids in Britain (Crawley, pers. comm.), although the reasons for this decline are unknown. Yet, low D_{ij} values between native and alien species, consistent with findings in 1995/96, suggest that apparent competition is unlikely to be an important driver of such declines.

The effects of changing dynamics on native species may be particularly important given the patterns of fluctuating populations of native cynipids from year to year. Several authors cite the possibility that long term population cycles are a feature of gall inducer population dynamics (both cynipid and non-cynipid), a factor which may explain fluctuating population dynamics (Schönrogge *et al.*, in prep). In a seven-year study on *Cynips divisa*, Gilbert *et al.* (1994) suggest that they might have captured one cycle from peak to peak. They also discuss other reported systems in which cycles are likely, including the cynipid gallwasps *Xanthoteras politum* (Washburn & Cornell, 1981), *Cynips quercusfolii* (Wiebes-Rijks & Shorthouse, 1992), and *Disholcaspis cinerosa* (Frankie *et al.*, 1992), and pemphigid aphids on *Pistacia* (Wool, 1990) and *Populus* (Moran & Whitham, 1988). A long term study of the gall midge *Taxomyia taxi* (Cecidomyiidae) showed that hemivoltine *T. taxi* populations and the parasitoid *Torymus nigratarsus* participate in a coupled interaction that regulates the population of both via delayed density dependence, resulting in cycles of at least 14 years (Hunter and Redfern, 2005). However, it is also true that indirect interactions may be particularly important for rare species, which should be most sensitive to even small increases in parasitoid pressure, but which are also most likely to be under-recorded in quantified web studies (Müller *et al.*, 1999; Schönrogge and Crawley, 2000). Where native galls are locally rare, increased parasitoid pressure via indirect interactions may have the potential to result in local extinction of native cynipid species.

Analyses of the quantitative webs can be used to answer the following questions outlined in the introduction:

1. Have attack rates for parasitoids of invading gallwasps changed over the last 10 years?

Some significant changes in the attack rates for parasitoids of invading gallwasps have occurred since 1995. The most notable change is in the increase in the attack rate of *M. fuscipes* and *M. tibialis* on the catkin galls of *A. quercuscalicis*. The attack rate of *M. fuscipes* has increased by 3 orders of magnitude when compared with 1995 quantitative webs and *M. tibialis*, which was not recorded from *A. quercuscalicis* in 1995, has become a dominant member of the parasitoid assemblage of *A. quercuscalicis* galls.

Comparing the species recorded from asexual *A. quercuscalicis* galls in 1995 and 2005, the attack rates for most species of inquilines and parasitoids at both Silwood and Puttenham are approximately one order of magnitude less than attack rates recorded in 1995. No other asexual autumn generation galls produced parasitoids or inquilines from which comparisons of attack rates could be made.

Comparisons of the attack rates at northern sites between 1995 and 2005 were limited at Beaulieu due to a lack of parasitoid emergence in sexual generation galls in spring and no invading asexual galls being recorded in autumn. Timing of collection could affect the number and species richness of parasitoids produced from rearings, particularly for spring bud galls. *Mesopolobus fuscipes* recorded from spring sexual generation bud galls at Beaulieu in 1995 is a late instar pupal parasitoid and it is possible that galls from Beaulieu in 2005 were collected too early to detect accurate levels of parasitoid attack. At Dunrobin in 2005, attack rates of *M. fuscipes* from *A. kollari* were 2 orders of magnitude lower than those recorded at the same site in 1995. There are no clear explanations for the lower attack rates observed in most species and it must be remembered that these results are extrapolated from random sampling of the population. An additional explanation for the lower attack rates could be the significant changes in the gall densities recorded at both Beaulieu and Dunrobin in 2005 compared with 1995, the changes in host density also affecting parasitoid populations attacking available galls.

2. Has the arrival of new invasive species altered the extent to which parasitoid communities focused on native and invading gallwasps interact?

Following the establishment of 4 more cynipid species to southern Britain, new links have been formed via shared parasitoids and inquilines between cynipid gall communities that were not previously detected and the number of links within the communities have increased. Most importantly, parasitoids attacking one of the newest invaders (*A. grossulariae*) break down host tree-associated trophic compartmentalisation. Data prior to the invasion of the 4 cynipid species studied (*A. aries*, *A. lucidus*, *A. grossulariae* and *Aphelonyx cerricola*) (Schönrogge and Crawley, 2000) showed that the parasitoid assemblages associated with the galls of the sexual generations of the alien species on *Q. cerris* were isolated and shared no, very few or weak links with the assemblages associated with native galls on *Q. robur*.

The arrival of the invader *A. grossulariae* has resulted in considerable overlap between communities associated with *Q. cerris* and *Q. robur*. At both Silwood and Puttenham, 6 species of parasitoid are now shared between native cynipids on *Q. robur* and invading cynipids on *Q. cerris*. The galls of the sexual generation of *A. grossulariae*, however, have currently recruited parasitoid species shared with native species on *Q. robur* rather than with the other invading galls on *Q. cerris*. As a community, this has increased the linkage density and species richness. As this study represents a snapshot in time, it has to be seen whether the community associated with *A. grossulariae* changes as the residency time of this gall in Britain increases, particularly given the fact that this invading gall was first recorded in Britain relatively recently (Walker, 2001).

An alternative scenario can be observed by comparing parasitoids attacking established invaders (*A. lignicolus*, *A. kollari* and *A. quercuscalicis*) on *Q. cerris* in spring with those attacking native galls on *Q. robur*. Currently, parasitoids of invading galls found on *Q. cerris* in spring are largely specialised to attack these invading gall types on *Q. cerris*. For example, *Mesopolobus tibialis* is a common parasitoid of spring sexual galls

of invading cynipids found on *Q. cerris*, but very few individuals have been reared from native galls on *Q. robur*, therefore *M. tibialis* is now a specialist parasitoid almost entirely restricted to *Q. cerris* galls.

The three recently invading cynipids *A. lucidus*, *A. aries* and *Aphelonyx cerricola* are currently relatively rare at both Puttenham and Silwood and were recorded at low densities during this study. As the density of these and the most recent invaders (*Plagiotrochus australis*, *P. coriaceus*, *P. quercusilicis* and *Neuroterus saliens*) increase and assemblages of parasitoids and inquilines associated with these galls develop, interactions between cynipid galls will also have the potential to increase in both strength and number. It can be hypothesised that parasitoid assemblages associated with invading gall types will stabilise over time and that some parasitoid species might specialise in attacking invading gall types, as appears to be the case with *M. tibialis* attacking *Q. cerris* spring sexual galls. Establishment of the *Plagiotrochus* species would be of particular interest, since these exploit a host – holm oak, *Q. ilex*, that supports no other gall inducing cynipids in the U.K.

In northern Britain, no new links were found within cynipid gall communities largely due to the decrease in the number of cynipid species recorded at both Beauly and Dunrobin in 2005/6 compared with 1994/5. This is shown by the much simpler webs and linkage diagrams generated for these northern sites compared with southern webs (where there are 6 more species of invading cynipids) and webs generated in 1994/5, when a much higher species richness of native cynipid species were recorded at these sites.

3. Is apparent competition important in structuring the cynipid communities post-invasion?

The low d_{ij} values, measuring the strength of indirect interactions, indicate that apparent competition is not important in structuring cynipid communities when considering

parasitoids shared between invading and native cynipid communities. Most of the d_{ij} values were below < 0.1 (13 of 20 values) and two values were >0.4 . In 1995, d_{ij} values were low everywhere ($<0.001 - 0.47$). However, in 2005, one exceptionally high value of 0.8910 was recorded for the community shared between the spring galls of the invading cynipid *A. grossulariae* and the autumn galls of another invader, *A. quercuscalicis* at Silwood Park. This high value results from the sharing of 4 parasitoids (*E. brunniventris*, *M. dorsalis*, *C. fungosa* and *E. urozonus*) between the 2 gall types.

The 2005-6 webs suggest that invading gallwasp species have little impact on native species through shared parasitoids. There are also currently no strong interactions between native parasitoids. However, as the density and species richness of invading cynipids increases throughout Britain, the potential for indirect interactions between invaders and also between invaders and natives may increase.

Predicted changes in climate and the possibility of global warming may also have the potential to influence invading cynipid populations in the future. *Q. cerris* is a non-native tree species at the edge of its range in Britain. To date, this species is found throughout Britain with the exception of north-west Scotland (Walker *et al.*, 2002). North of the central belt of Scotland, the *Q. cerris* distribution is fragmented, typically being isolated and restricted (see map, Chapter 3, Figure 2.1). This fragmentation of the obligate host may slow or limit cynipid invasion to northern Scotland (see Chapter 2, Discussion). While regeneration of *Q. cerris* is widespread in southern England, it is very limited in northern Scotland (Walker *et al.*, 2002). Should predicted global temperature increases occur, a more favourable climate may facilitate regeneration and increase *Q. cerris* density, particularly in northern Britain, increasing the potential for range expansion of invading cynipid gall species in Britain. Fossil galls for species inferred to have host alternating lifecycles have been found far to the north of their current native ranges in Europe, indicating a more northern limit for host-alternating gallwasps in the past (Kortselius *et al.*, 2007). These same arguments apply even more to gallwasps associated with holm oak, *Q. ilex* and cork oak, *Q. suber*. Both support rich

communities of cynipids in circummediterranean habitats (Nieves-Aldrey, 2001). Very few records exist for gallwasps on these oaks in northern Europe, although *Q. ilex* is widely distributed across this range, including many parts of Britain.

Chapter 5

Patterns of bird predation of the sexual generation bud galls of invading cynipids in Britain

5.1 Introduction

Many factors, both biotic and abiotic, can influence populations of organisms. These include natural enemies, competitors, nutrient availability, pathogens and climate (Hunter and Price, 1992). The relative extent to which phytophagous insect populations are constrained by natural enemies (top-down effects) or by plant resources (bottom-up effects) has been the subject of much research and debate (Washburn and Cornell, 1981; Hunter and Price, 1992; Roininen *et al.*, 1996; Ylioja *et al.*, 1999; Hawkins *et al.*, 1999; Price, 2002). The chestnut gallwasp *Dryocosmus kuriphilus*, a pest species in Japan, USA and parts of Europe provides an example of top-down control by natural enemies. *Dryocosmus kuriphilus* declined significantly following the introduction of the parasitoid *Torymus sinensis* from the native range of China (Washburn and Cornell, 1981; Moriya *et al.*, 1989; Schönrogge *et al.*, 1999; 2006; Aebi *et al.*, 2007). Other studies provide evidence of bottom-up control. Long-term studies on galling sawflies have found a general pattern of strong bottom-up influences through plant quality to stem and bud galls in the genus *Euura* and its parasitoids (Roininen *et al.*, 1996; McGeoch & Price 2005). Some studies have found support for both bottom-up and top-down effects. A long-term study of the wood-mining agromyzid, *Phytobia betulae*

(Diptera: Agromyzidae) showed that both the age of the wood resource (bottom-up) and parasitoid attack (top-down) could influence population dynamics (Ylloja *et al.*, 1999).

Theoretical population dynamics of herbivorous insects are based largely on the assumption that the top-down influence of density dependent parasitism or predation regulates populations of herbivorous insects (Holt, 1977; 1984; Hassell, 1978; Schönrogge *et al.*, 1999). Spatial density dependence is important because numerous studies have suggested that it can contribute to both the regulation and stability of predator-prey and host-parasitoid systems (Hassell, 1985; Hassell and Pacala, 1990; Hassell *et al.*, 1991; Redfern *et al.*, 1992; Hails and Crawley, 1992; Jones *et al.*, 1993; Schönrogge *et al.*, 1999; van Veen *et al.*, 2002; Matsumoto *et al.*, 2004). Spatial aggregation of deaths can have a stabilising effect on population dynamics if it creates a refuge which translates into temporal density dependence (Hassell, 1985). The refuge may result from increased mortality in patches of either low or high host density, or from heterogeneity in the risk of death that is density independent (i.e. associated with environmental factors other than local population density) (Hails and Crawley, 1992). The key point is that spatial density dependence must bring about temporal density dependence if it is to exert a regulatory influence on host population density (Hails and Crawley, 1992). Compared with spatial density dependence, temporal density dependence is particularly difficult to detect (see Chapter 1, Section 1.7).

Evidence concerning cynipid gallwasps is currently ambiguous (Schönrogge *et al.*, 1999) and has been almost exclusively focused on examining the relationship between gallwasps and parasitoid species that attack them. Population studies of the sexual generation of the invading gallwasp *Andricus quercuscalicis* failed to produce consistent evidence of spatially density dependent parasitoid attack, suggesting that the choice of the appropriate spatial scale to be analysed is important (Hails and Crawley, 1992; Veldtman & McGeoch, 2004). Employing a hierarchical sampling scheme (shoots within branches within trees within sites), relationships between gall density and

parasitoid attack rates were found to be positively, negatively or spatially density independent with no consistent pattern (Schönrogge, 1994).

While density dependent parasitism has been studied in cynipid gallwasps by examining the impacts of parasitoids that attack them, an equivalent study of spatial density dependent predation by birds has not been conducted to date. Bird predation as an additional source of mortality has received limited attention (Askew, 1961; Schönrogge *et al.*, 1994; 1996; 1999; Stone *et al.*, 1995; Plantard and Hochberg, 1996). The bud galls of the sexual generations of invading gall species found on *Quercus cerris* are often opened by birds, particularly blue tits (*Parus caeruleus*) and great tits (*P. major*) (Schönrogge *et al.*, 1999). Bird predation may impact on gallwasp population dynamics in addition to mortality induced by insect parasitoids, with potentially important implications for our understanding of the dynamics of gallwasp populations.

Analyses for this study were restricted to bud galls, where bird predation can be reliably detected. Catkin galls are not included as catkins are likely to be removed entirely by the birds. Four species of invading cynipid gallwasps that cause bud galls in *Q. cerris* in spring are currently found within Britain: *Andricus kollari*, *Andricus lignicolus*, *Andricus corruptrix* and *A. aries*. These species are currently at different stages in their invasion of Britain, reflected in the extent of their northern advance across the country (see Chapter 2). The sexual generation bud galls of *A. aries* have not been formally described, but have been described informally as small reddish bud galls (GN Stone pers. comm. from Pat Walker). No galls of this type were detected in my surveys, and my data are thus restricted to *Andricus kollari*, *Andricus lignicolus* and *Andricus corruptrix*.

In spring, the sexual generations of *A. corruptrix*, *A. kollari* and *A. lignicolus* induce small morphologically similar galls less than 5 mm in diameter in the buds of *Q. cerris*. Gall development begins in February. Immature galls are soft and green and harden and darken during development. The number of bud galls that develop can vary between

species and between one and seven galls develop within one bud. *Andricus corruptrix* galls are almost always found singly, *A. lignicolus* often in clusters of 2 - 3 galls per bud, while *A. kollari* induces up to 7 galls per bud. All of these bud galls mature in April and become most visible as the buds begin to develop and grow prior to bud burst. Previous studies of invading gallwasps at sites across Britain found evidence that bird predation caused significant mortality (max. 59.2%) in the sexual bud gall *A. kollari* at Silwood Park in the south of Britain (Schönrogge *et al.*, 1999).

In this study, we assess the evidence for density dependent bird predation at a range of different spatial scales, and address the following questions and hypotheses 1) Is there evidence of spatially density dependent predation of bud galls by birds and if so, at what scale? 2) Where spatial density dependence is detected, I ask which of two alternative hypotheses of change over the course of a single season is supported. (a) Does density dependence become stronger as predation accumulates? (b) Alternatively, does spatial density dependence weaken as host patches become rarer over time?

5.2 Methods

5.2.1. Selection of sites and trees

I examined bird predation of bud galls on *Q. cerris* at 3 different spatial scales: on trees within sites, on branches within trees, and on shoots within branches within trees. Here I analyse 2 discrete datasets. (a) Previously unpublished data collected at 8 sites across Britain in 1995 (b) data collected in spring 2006 on a weekly basis for 5 weeks from one site in south east England (Puttenham Common). This second data allows me to analyse temporal development of bird predation patterns through a single season.

(a) Quantitative samples collected from 8 sites across Britain in 1995

For the data collected in 1995, 4 geographical zones were then defined based on the number of invading cynipid species present within each zone and 8 sample sites were selected (Schönrogge *et al.*, 1996) (see Chapter 1, Figure 1.5, Section 1.6). In each of the 4 zones, 2 sites were chosen using the following criteria as applied by Schönrogge *et al.*, 1996; 1998; 1999: (i) the sites had to be at least 50km apart; (ii) the host oak species, *Q. cerris* and at least one of the native species, *Q. robur* or *Q. petraea*, had to be present; (iii) the oak stands had to be sufficiently large to allow a minimum of 6 trees to be selected at random for each host species (Schönrogge *et al.*, 1996; 1998; 1999). For each of these 8 sites, the distribution and size structures of the oak stands are given by Schönrogge *et al.* (1998) (see Appendix, Table 7.3).

Twelve trees were selected at random from marked cohorts of suitable *Q. cerris* at Silwood Park, Puttenham Common, Tatton Park, Rufford Park and Falkland. At the 3 remaining sites, the number of trees selected was limited by the number of *Q. cerris* available. At Erskine, 9 trees were selected, at Beaulieu 10 trees and at Dunrobin, 7 trees.

(b) Quantitative samples collected over 5 weeks at Puttenham Common during spring 2006.

In 2006, a further 12 trees were selected at Puttenham Common in order to examine within-site predation of bud galls by birds during the pre-breeding period. Data were collected over a five week period from the last week of March until the end of April as spring bud galls develop to maturity on *Q. cerris*.

5.2.2. Randomised sampling of shoots

Samples of 15 branches in 1995 and 10 branches in 2006 were taken from various aspects and heights from each of the selected sample trees using a pole pruner to give a

reach of approximately 8 metres. A branch represents 4 years of discrete growth and can be identified by the number of ring scars (Schönrogge *et al.*, 1998). Six shoots (defined as last year's growth) were then chosen at random from every branch and the number of galls and buds, either intact or predated, were counted. Bud galls of invading cynipid species on *Q. cerris* are very small and concealed within the buds, so *Q. cerris* shoots were dissected in the laboratory.

5.2.3. Bird counts – Puttenham Common, spring 2006

Based on total gall counts per tree recorded from trees during the first week of collection in spring 2006, 3 trees were designated as trees with a high density of galls and 3 as trees with a low density of galls. On each of the subsequent 4 visits to Puttenham Common each of the 6 trees was observed for 1 hour and the species and numbers of birds observed within the trees were counted during this time.

5.2.4. Statistical modelling

Nested analyses of density dependence on the proportion of galls that showed signs of predation were carried out using generalised linear models (GLMs) in S-Plus with binomial errors and a logit link function. Means were calculated in a hierarchical manner throughout, branch means from shoots and tree means from branch means to avoid pseudo-replication in the GLMs.

Model terms were tested for significance on deletion and the model simplified until all retained terms were significant (minimum adequate model; Crawley 2004). All models were inspected for overdispersion (models with binomial errors) and checked for heteroscedasticity and the normality of errors (Crawley 2004).

5.3 Results

5.3.1. Variation in levels of bird predation on galls

While I will report the results for all the sites and trees as appropriate, because of the complex datasets used I will concentrate on the southern sites, and particularly Puttenham Common (where data from both 1995 and 2005 were available, to illustrate the results).

There was considerable variation in the levels of bird predation among trees (Silwood 1995: average proportion: range 0.15 ± 0.09 - 0.71 ± 0.06 ; Puttenham Common 1995: 0.07 ± 0.05 - 0.36 ± 0.09), between sites (Silwood 1995 site mean: 0.53 ± 0.02 ; Puttenham Common 1995 site mean: 0.20 ± 0.02), and between years (Puttenham Common 2005 site mean: 0.41 ± 0.03 ; tree mean range: 0.29 ± 0.11 - 0.79 ± 0.07). At some sites a few of the randomly selected trees produced no galls with the sample size used. However, at all scales investigated here there is sufficient variation in bird predation levels to consider spatial density dependent patterns.

Using a nested ANOVA (GLM with binomial errors and logit link) to partition the variance between branch (nested within trees) and tree levels, Tree as a hierarchical level consistently explains more of the deviance in the levels of bird predation than Branch within Tree (Silwood 1995 Tree: 33.3% - Branch: 20.7%; Puttenham Common 1995 Tree: 21.1% - Branch: 10.7%, and Puttenham Common 2005 Tree 23.8% - Branch 21.9%). Analysing bird predation at tree level might provide more power, however, as previous studies indicate the consistency of the signs of relationships are equally important to understand patterns of bird predation. To do so, regression models were fitted at the appropriate spatial scale.

5.3.2. Spatial density dependence in bird predation

Three models were used to determine whether bird predation of galls showed spatial density dependence by examining the relationship between the proportion of galls predated and gall density at different spatial scales from shoots (within branches within trees), to branches (within trees) and finally, regressions across trees.

The models were applied to data from all 8 sites studied in 1995, but also to the weekly sampling carried out over 5 weeks at Puttenham Common in 2005.

(a) Patterns of spatial density dependence at eight sites in Britain

At the smallest spatial scale, shoots within branches within trees, significant overall results were found at 6 of the 8 sites, more than at the branch (within tree) or tree scale with one and two significant results respectively (Table 5.1). However, consistency in the sign of any correlations found is given in Table 5.1 as the proportion of positive regressions. At the shoot scale that proportion is variable ranging from 0.64 – 0 or, considering only the significant correlations, from 0.64 – 0.18 (mean 0.39 ± 0.06) (Table 5.1). At the branch (within trees) level correlations are more consistently positive, yet only one (Dunrobin) is significant and here only 14% are positive.

Finally at the tree level only the 2 most southern sites show significant regressions, yet in both cases they are positive (Table 5.1). Of course, across trees there is only one regression at each site and thus the proportion positive can be only 0 or 1. However, that tree is the hierarchical level at which birds might recognise gall densities, is consistent with the partitioning of deviance (above), and might also be suggested by the fact that the amount of deviance explained by the tree models is generally higher than that explained at the shoot or branch scale (Table 5.1).

Table 5.1 Summary statistics for the GLMs used to analyse data collected from 8 sites across Britain in 1995. ns = not significant.

	Residual Deviance	d.f.	Overall deviance	d.f.	% Deviance explained	F-value	P	Proportion +ve regressions
Model 1 (Shoots within branches within trees)								
Site								
Silwood Park (1)	158.83	82	837.33	1049	19	1.71	P<0.01	0.64
Puttenham (2)	201.82	46	365.93	1061	55	2.34	P<0.001	0.34
Tatton Park (3)	26.28	22	164.92	1040	16	3.4	P<0.01	0.18
Rufford (4)	45.36	30	401.70	1028	11	1.88	P<0.05	0.44
Erskine (5)	45.25	20	177.18	805	26	1.7	ns	0.4
Falkland (6)	74.05	32	335.86	961	22	2.6	P<0.01	0.55
Beaully (7)	19.82	26	112.02	864	18	12.0	P<0.01	0.23
Dunrobin (8)	2.19	37	27.74	614	8	1.19	ns	0
Model 2 (Branches within trees)								
Site								
Silwood Park (1)	1.82	11	83.44	179	2	0.55	ns	0.73
Puttenham (2)	4.91	11	40.86	179	12	1.44	ns	0.73
Tatton Park (3)	3.46	11	22.02	179	16	1.43	ns	0.09
Rufford (4)	5.89	11	55.34	179	11	1.37	ns	0.64
Erskine (5)	1.48	8	17.12	134	9	0.76	ns	0.75
Falkland (6)	3.16	11	42.21	178	7	0.83	ns	0.55
Beaully (7)	0.50	8	16.29	149	3	0.18	ns	0
Dunrobin (8)	1.82	7	4.30	104	42	<0.01	P<0.001	0.14
Model 3 (Within trees)								
Site								
Silwood Park (1)	2.08	1	2.66	11	78	16.89	P<0.001	1.00*
Puttenham (2)	0.19	1	0.41	11	46	9.26	P<0.001	1.00*
Tatton Park (3)	0.04	1	0.23	11	17	1.93	ns	0
Rufford (4)	0.19	1	0.91	11	21	2.81	ns	1.00*
Erskine (5)	0.0003	1	0.95	8	<0.1	0.25	ns	0
Falkland (6)	0.03	1	0.57	11	5	0.49	ns	1.00*
Beaully (7)	0.02	1	0.18	9	11	1.19	ns	0
Dunrobin (8)	0.06	1	0.17	6	33	2.02	ns	0

*For Model 3, there is only one regression at each site therefore this proportion can only be 1 or 0.

(b) Patterns of spatial density dependence over time at Puttenham Common, spring 2006

Weekly samples were taken over 5 weeks at Puttenham Common to assess the temporal pattern that would be expected if bird predation accumulates over a period of weeks. Two alternative hypotheses for predicted changes are (a) that patterns of spatial density dependence will become stronger as predation accumulates, or (b) that it will become weaker as high density patches become rare. As in 1995, the sampling at Puttenham Common over 5 weeks shows considerable variation among trees in both gall densities and predation rates (Table 5.2). For instance, in week 2, gall densities ranged from 0.08 galls per shoot on tree 12 to 1.6 galls per shoot on tree 8 (Table 5.2) and similarly, predation rates varied between 0% and 81%. Unexpectedly, over the five weeks leading up to the emergence period of the gallwasps, the proportion of galls per shoot in the population declined from $71\% \pm 0.04$ to $35\% \pm 0.03$, i.e. the density effectively halved (Figure 5.1).

Figure 5.1 The proportion of buds galled per shoot (\pm S.E.) and predation rates (proportion galls pecked) measured in the 5 sampling weeks.

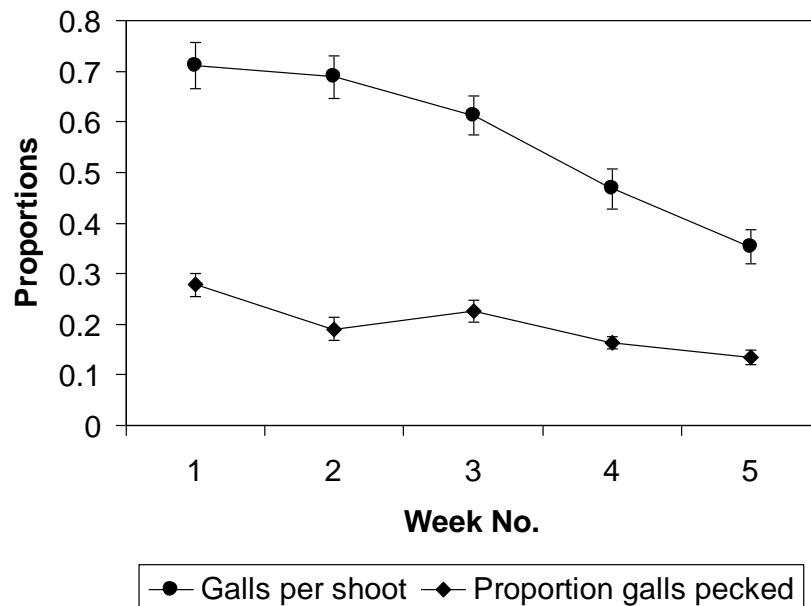


Table 5.2 Gall densities and predation rates per tree measured on each of the 12 sample trees at each of the 5 sampling dates.

Tree	Week									
	1		2		3		4		5	
	Density	Predation	Density	Predation	Density	Predation	Density	Predation	Density	Predation
1	0.73	0.16	1.27	0.58	0.68	0.15	0.12	0.28	0.22	0.23
2	1.3	0.81	1	0.53	0.78	0.51	0.2	0.5	0.25	0.47
3	0.36	0.36	0.43	0	0.38	0.56	0.13	0.13	0.12	0
4	0.13	0.38	0.12	0	0.16	0	0.16	0	0.08	0
5	1.5	0.59	1.7	0.55	1.5	0.55	1.1	0.29	1.1	0.32
6	0.92	0.27	0.68	0	0.55	0.06	0.58	0.15	0.18	0.08
7	0.8	0	0.57	0	0.65	0	0.98	0.17	0.27	0
8	1.6	0.48	1.1	0.51	1.5	0.63	1.4	0.23	1.2	0.36
9	0.78	0.28	0.83	0.12	0.65	0.26	0.76	0.21	0.63	0.16
10	0.18	0	0.43	0	0.18	0	0.1	0	0.17	0
11	0.16	0	0.1	0	0.12	0	0.08	0	0	0
12	0.08	0	0.03	0	0.2	0	0	0	0.01	0

Predation rates declined over the 5 week period from an average of $27.8\% \pm 0.02$ to $13.5\% \pm 0.01$. However, Spearman Rank correlations suggest that the between-tree structure in densities and predation rates is maintained despite the overall change (Table 5.3).

Table 5.3 Between week pairwise Spearman Rank Correlation Coefficients (R^2). The upper matrix shows rank correlations in gall density and the lower matrix the R^2 values for predation rate correlations. All correlations except 1 (predation rates between week 1 & 2 $p = 0.052$) are significant at $p < 0.05$, in fact those for densities are all $p < 0.01$, and had 10 degrees of freedom.

		Density				
		Week 1	Week 2	Week 3	Week 4	Week 5
Predation rate	Week 1		0.72	0.78	0.73	0.79
	Week 2	0.32		0.83	0.48	0.75
	Week 3	0.57	0.38		0.55	0.82
	Week 4	0.41	0.77	0.49		0.79
	Week 5	0.51	0.77	0.51	0.81	

In fact the rank order between gall densities in trees and predation rates were also positively correlated (week 1: $R^2 = 0.36$, $p < 0.05$; week 2: $R^2 = 0.78$, $p < 0.001$; week 3: $R^2 = 0.56$, $p < 0.01$; week 4: $R^2 = 0.42$, $p < 0.05$; week 5: $R^2 = 0.56$, $p < 0.01$; d.f. was 10 for all analyses), lending further support that at the scale of trees, bird predation is positively spatial density dependent and that the pattern can be detected over a period of time.

To assess whether the declines in gall density and predation rates might affect patterns of spatial density dependence differently at different spatial scales, GLMs equivalent to those used for the 1995 data (Table 5.1) were fitted to the data from Puttenham Common treating each week separately (Table 5.4). In contrast to the 1995 data, at the smallest scale of shoots (within branches within trees), only one of the 5 analyses provided an overall significant result (week 5) and the amount of deviance explained by any of the

models tends to be small (< 25%). Also, in week 5, fewer than 30% of the correlations within branches were positive (Table 5.4). At the scale of branches (within trees) the results are similar. In fact, none of the analyses yielded a significant overall result, the signs of the coefficients are mixed and the amount of deviance explained is small (<25%; Table 5.4).

In contrast, at the tree level there were significant positive relationships in weeks 1 – 3 (note that at tree level there is only 1 correlation and “proportion +ve regressions” in Table 5.4 can only be 1 or 0) and the amount of deviance explained (44% - 65%) is considerable and higher than at the smaller spatial scales. There are no significant correlations in week 4 and 5 when gall densities and predation rates had declined.

5.3.3. Predators of galls, Puttenham Common spring 2006

During the one hour observation of the three trees with high and low gall densities, 7 species of birds were observed pecking at buds on *Quercus cerris*: blue tit (*Parus caeruleus*), great tit (*Parus major*), long-tail tit (*Aegithalos caudatus*), robin (*Erithacus rubecula*), song thrush (*Turdus philomelos*), blackbird (*Turdus merula*), and green woodpecker (*Picus viridis*). The incidence for all the species was low, although blue tits were recorded most often (47 records over all trees and observation periods) (Table 5.5). Because of the low incidences it would be inappropriate to try and distinguish between low and high density trees. For blue tits, the incidences on high and low density trees were pooled over the 4 recording events. The average number of observations on high density trees was 8.7 ± 0.05 compared to 7.0 ± 0.08 on low density trees ($t = 2.4$, d.f. 4, $p = 0.066$). With such low numbers of counts and replicate trees the confidence in this difference is limited. However, based on the higher abundance of blue tits and a strong trend (significant at the 6.6% level) it seems likely that this species is mostly responsible for the patterns in bird predation described above.

Table 5.4 Summary statistics for the GLMs used to analyse data collected from Puttenham Common in 2006. ns = not significant.

	Residual Deviance	d.f.	Overall deviance	d.f.	% Deviance explained	F-value	P	Proportion +ve regressions
Model 1 (Shoots within branches within trees)								
Week								
1	97.52	47	520.27	719	19	1.32	ns	0.35
2	52.52	53	407.42	719	13	0.93	ns	0.28
3	52.76	41	344.92	719	15	1.39	ns	0.23
4	60.27	38	270.83	719	22	1.17	ns	0.20
5	51.14	27	222.92	719	23	1.87	<0.05	0.28
Model 2 (Branches within trees)								
Week								
1	5.33	11	53.88	119	10	1.67	ns	0.46
2	0.78	11	45.80	119	2	0.33	ns	0.27
3	2.70	11	36.86	119	7	1.62	ns	0.18
4	5.12	11	24.79	119	21	1.69	ns	0.45
5	4.03	10	19.80	119	20	2.09	ns	0.20
Model 3 (Within trees)								
Week								
1	1.20	1	2.75	11	44	8.30	<0.05	1.00*
2	1.98	1	3.07	11	65	21.37	<0.001	1.00*
3	1.28	1	2.44	11	52	10.90	<0.01	1.00*
4	0.06	1	0.56	11	11	0.68	ns	1.00*
5	0.34	1	0.73	11	47	3.67	ns	1.00*

*For Model 3, there is only one regression at each site therefore this proportion can only be 1 or 0.

Table 5.5 Bird species recorded by week in each of the 6 trees; 3 high gall density (HD) and 3 low density (LD) trees over the 4 week observation period.

		Week								
		2		3		4		5		Total
Tree	Bird species present	n	Bird species present	n	Bird species present	n	Bird species present	n	n	
HD1	blue tit	4	blue tit	2	blue tit	0	blue tit	3	9	
	great tit	1	great tit	0	great tit	2	great tit	0	3	
	robin	1	robin	0	robin	0	robin	1	2	
	song thrush	0	song thrush	0	song thrush	1	song thrush	0	1	
	blackbird	1	blackbird	0	blackbird	0	blackbird	0	1	
HD2	blue tit	2	blue tit	0	blue tit	3	blue tit	4	9	
	great tit	0	great tit	2	great tit	1	great tit	0	3	
	robin	0	robin	1	robin	0	robin	1	1	
	song thrush	0	song thrush	0	song thrush	1	song thrush	0	1	
	green. woodpecker	0	green. woodpecker	0	green. woodpecker	1	green. woodpecker	0	1	
	blackbird	1	blackbird	0	blackbird	0	blackbird	0	1	
HD3	blue tit	3	blue tit	1	blue tit	1	blue tit	3	8	
	great tit	0	great tit	1	great tit	0	great tit	1	2	
	robin	0	robin	0	robin	0	robin	1	1	
	blackbird	1	blackbird	0	blackbird	0	blackbird	0	1	
LD1	blue tit	2	blue tit	1	blue tit	3	blue tit	1	7	
	great tit	0	great tit	2	great tit	0	great tit	1	3	
	robin	1	robin	0	robin	0	robin	1	2	
	blackbird	1	blackbird	0	blackbird	0	blackbird	0	1	
	long-tailed tit	0	long-tailed tit	4	long-tailed tit	0	long-tailed tit	0	4	
LD2	blue tit	2	blue tit	2	blue tit	3	blue tit	1	8	
	robin	0	robin	0	robin	1	robin	0	1	
	song thrush	1	song thrush	0	song thrush	0	song thrush	0	1	
	blackbird	0	blackbird	0	blackbird	1	blackbird	0	1	
LD3	blue tit	0	blue tit	2	blue tit	1	blue tit	3	6	
	great tit	1	great tit	1	great tit	0	great tit	0	2	
	robin	0	robin	0	robin	1	robin	0	1	
	song thrush	0	song thrush	0	song thrush	0	song thrush	1	1	

5.4 Discussion

5.4.1. Evidence of spatial density dependence in bird predation

(a) Data from multiple sites across Britain, 1995

The data from the 8 sites across Britain provide some support that positive spatial density dependence in bird predation of bud galls occurs at the scale of the tree. This conclusion is consistent with the partitioning of deviance and is also suggested by the fact that the amount of deviance explained by the tree models is generally higher than that explained at the shoot or branch scale. However, regression analyses show that only the two most southern sites (Silwood Park and Puttenham Common) show significant positive regressions at the tree scale. Results from other sites are less consistent, showing variation either in numbers of significant regressions or varying proportions of positive regressions for each of the spatial scales examined. Evidence supporting the existence of spatial density dependence based on the regression analyses at these other sites is therefore equivocal.

(b) Data from multiple weeks, Puttenham Common, 2006

Results from the weekly random sampling from Puttenham Common are more consistent and show that positive spatial density dependence in bird predation of bud galls occurs at the scale of the tree. Further support for positive spatial density dependence of bud galls at the level of the shoot is provided by the fact that the rank order between gall densities per tree and predation rates were positively correlated and that this density dependence can be detected over a period of time.

Intriguingly, there are no significant correlations in week 4 and 5 when gall densities and predation rates had declined. It was hypothesised that as bird predation accumulates over the weeks that patterns of density dependence would either become stronger, or, alternatively, become weaker as high density patches become rarer (i.e. predation levels reach an upper threshold as all high density patches have been

exploited, and it thus becomes difficult to still find significant relationships in the data). Although the data lend more support to the second hypothesis - since correlations change from being significant (weeks 1 – 3) to not significant (weeks 4 and 5) - ultimately neither hypothesis can legitimately be supported by these data since the decline in gall densities makes this interpretation ambiguous and a lack of significant correlations could arise if the decline in predated and un-predated galls is not proportional.

The decline in the density of galls by approximately half across the period of data collection is unexpected and the reasons for this decline can only be speculated. Buds containing galls may, during the course of bud development prior to bud burst, undergo abscission as an induced oak response to the presence of bud galls, i.e. these buds containing galls may have inhibited development and represent a poor investment for the tree. Buds with intact galls (not predated) could be more of a sink to the tree and are more likely to be aborted. If that was the case, it can be predicted that intact galls would be disproportionately lost compared to predated ones. The sessile lifestyle of gallers appears to make abscission a likely mechanism of defence and has also been reported in a number of galling insects including aphids, psyllids and cecidomyiids (Williams and Whitham, 1986; Yukawa and Tsuda, 1986; Fernandes *et al.*, 1999; Wool and Bogen, 1999; Stromgren and Lanciani, 2001; Espirito Santo and Fernandes, 2002, Fernandes *et al.*, unpubl.).

The geographic pattern of significant relationships in the south but the lack of it in the northern populations has an intriguing parallel with the geographic pattern of parasitoid recruitment (see Chapter 3) and might reflect the residence time of the invading species. Although bird predation occurs in northern populations, it is possible that the birds have to experience a number of generations of consistent, high density supplies of this novel early season protein source before they learn how to exploit it. If so, one would predict that spatial density dependence should be detectable in more northern populations in the future, just as Chapter 3 describes the northern movement of the recruitment front for inquiline and parasitoids.

The most abundant bird species recorded at Puttenham Common was the blue tit. Blue tits exploit a wide range of food items and their potential to regulate populations of bud galling cynipids must be seen in the context of the availability of alternative food sources (Schönrogge *et al.*, 1999). The mean laying date of blue tits is closely correlated with the date of oak bud burst (Slagsvold, 1976; Visser and Lambrechts, 1999). During the breeding season, blue tits feed predominantly on caterpillars and breeding success is closely linked with caterpillar abundance (Visser and Lambrechts, 1999, Visser *et al.*, 2002). These studies did not include *Q. cerris* bud galls as a potential food resource, and in fact we do not know whether *Q. cerris* trees were available at the study locations. Before caterpillars are available, gallwasps might provide a rare protein source. However, the decrease in predation rate of bud galls in April towards the onset of nest building and egg laying could result through blue tits switching from bud galls to alternative larger, more protein-rich prey, which would provide a higher reward for less energetic expense (Naef-Daenzer and Keller, 1999; Naef-Denzer *et al.*, 2004). The abundance of caterpillars relative to galls will also increase as spring progresses.

Density dependent predation of bud galls at the spatial scale of the tree can be detected at Puttenham Common in 2006. However, a study considering trees as patches for foraging blue tits found trees were not selected as patches based on food availability, patch quality or tree size (Pulido and Diaz, 1997). Instead Pulido and Diaz (1997) found bird abundance to correlate strongly with tree density and the availability of holes for nesting during the pre-breeding period. This is perhaps unsurprising since as a generalist predator, blue tits respond to a variety of factors which may in turn affect diet choice (Visser *et al.*, 2002). Within the UK, the use of galls on *Q. cerris* may, however, still be significant. This is the first study that I know of to specifically examine predation of cynipid galls by birds. The results of this study can therefore only be considered as a preliminary investigation. The results discussed indicate a need for further research. Suggestions for future research are made in Chapter 6 (see Section 6.3).

5.4.2. The potential effects of bird predation on gallwasp populations

Predation by birds can cause significant mortality in the sexual generation of bud galling cynipids. A maximum mortality of 63% was recorded at Puttenham Common in 2006. High predation rates were also recorded in a previous study at Silwood in 1995 (maximum 59.2%) (Schönrogge *et al.*, 1999). However, there are marked contrasts in the levels of predation recorded between trees with a high gall density and trees with a low gall density. Trees with a high density of galls showed disproportionately high levels of gall predation while trees with low gall density showed no evidence of bird predation of galls. This may indicate that a patch (i.e. a tree) is selected on the basis of the rewards available (the number of galls as a food source) in that patch and that birds are more likely to exploit higher quality patches (patches that provide higher energetic returns) for any given length of time spent foraging (Charnov, 1976; Parker and Stuart, 1976). Charnov's marginal value theorem (1976) proposes that the optimal stay-time should be greater in more productive patches and for the least productive patches, the stay-time should be 0. In Charnov's terms, trees with high gall densities would be regarded as more productive, since they provide a higher return to the foraging birds. The positive density dependent response to gall densities might suggest that they could become a significant part of the blue tit diet where gallwasp populations are stable and predictable.

Gallwasp populations further north, and closer to the invasion front, appear to be more variable in time (Chapter 4, Schönrogge *et al.*, 1999; Schönrogge & Crawley, 2000), and it remains to be seen whether bird predation will eventually become spatially density dependent further north. However, if spatial density dependence can have a stabilising effect on the hosts population dynamics, where behavioural adaptations by native predators to alien prey are required, stable and predictable population dynamics might be a pre-requisite (Hassell, 1985; Hails and Crawley, 1992). Also, additional consideration must be given to the relative abundance of alternative food sources in spring, and the fact that species exploiting bud galls as a

food source may assess patches according to reward and may require a threshold density of galls per patch before a patch will be exploited.

Positive spatial density dependence of bird predation might also affect the interactions between the bud galls on *Q. cerris* and their parasitoids. Four species of Pteromalid parasitoids have been recorded from the bud galls on *Q. cerris*: *Mesopolobus fuscipes*, *M. xanthocerus*, *M. tibialis* and *M. dubius* (see Chapter 3). These species are all late instar/pupal parasitoids of bud galling cynipids (Askew, 1961; Schönrogge & Crawley, 2000) and attack in the late stages of gall development. Data collected at Puttenham Common in 2006 show that predation rates are certainly not increasing late in gall development and the parasitoids are unlikely to suffer mortality by bird predation. However, bird predation is likely to change the distribution of suitable, i.e. unpredated hosts. We can hypothesise how bird predation might affect host-parasitoid interactions: (1) Potentially, parasitoids have a much reduced number of available hosts, consequently, the proportion of the remaining unpredated bud galls attacked by parasitoids in such circumstances may be higher (Koenig *et al.*, 1994; Schönrogge *et al.*, 1999). However, the smaller number of hosts would equally restrict the parasitoid population size, if, as for *Mesopolobus fuscipes*, no other hosts are used. (2) Alternatively, parasitoids and birds could act on different spatial scales, such that the impact of bird predation on parasitoid attack could be minimal. Little is known about the movement of parasitoids associated with galls, although they have been observed to move within a canopy by jumping from leaf to leaf rather than flying (Askew, 1961; 1984) and their range could be limited. If bird predation primarily reduces host aggregation between trees, this might not affect aggregation levels within trees as possibly experienced by the parasitoids (Hails & Crawley, 1991). (3) Birds and parasitoids could act on the same scale, such that spatially density dependent bird predation would also reduce the spatial aggregation of hosts as experienced by parasitoids. As a consequence, it might well not be adaptive for parasitoids to show spatially density dependent oviposition behaviour based on host densities before bird predation acts (Charnov, 1976). This gallwasp system may well be appropriate for future distinction between these alternatives.

The effects on host population dynamics of sequentially acting sources of mortality have rarely been considered theoretically, despite the fact that this situation probably occurs frequently where the host/prey moves between habitat compartments. For instance, acorns might first be attacked in the canopy by acorn weevils and then later on the ground by mice. One example of such a study is by Mouquet *et al.* (2005), which considers two types (contest and scramble) of intraspecific competition that occur sequentially during the larval development of the Lycaenid butterfly *Maculinea arion*. The population dynamics of *M. arion* are unlikely to be directly relevant to the predator/parasitoid – prey interactions discussed here. However, Mouquet *et al.* do demonstrate that the parameters of both interactions are sensitive to each other and can lead to complex dynamics including limit cycles, which are considered relevant for the population dynamics of galling insects (Gilbert *et al.*, 1994; Hunter & Redfern, 2005).

Chapter 6

Concluding remarks

6.1 The value of cynipid gallwasps as a study system

Cynipid gallwasps have provided, and will continue to provide an enormous wealth of avenues of research in the future. The question is: What are the most valuable lines of enquiry one should pursue in order to inform us most, not just about the status of invasions of cynipids and their associated communities, but how cynipids can be used as an appropriate model system to test and develop sound ecological theory in a wider context? This is a valid question, particularly for a PhD student with a relatively short and ultimately finite time in which to plan and conduct a coherent research program. As such, I have made suggestions specifically relating to my own studies below (Section 6.4, Future research). In terms of the cynipid galling system as a whole, fundamental questions still require to be answered. The way in which gallwasps induce gall formation on host plants remains an enigma. Despite the progress of molecular research, an understanding the molecular tools that cynipids use to manipulate plant development is limited. Also, gall traits such as structure, location and phenology may play important roles in community diversity, but there is little empirical evidence of this to date (Hayward and Stone, 2005).

6.2 Bird exploitation of galls – Broader implications for oak associated communities

Bird exploitation of alien galls has broader implications for oak-associated animal communities. Many of the parasitoid natural enemies that attack alien cynipid galls on Turkey oak also attack native oak gallwasps (Schönrogge & Crawley 2000), and the invaders may have negative impacts on natives through apparent competition mediated by shared parasitoids (van Veen *et al.* 2006; Cronin 2007). If birds predate galls before parasitoid natural enemies have a chance to emerge, they kill these parasitoids and reduce the potential for parasitoid-mediated apparent competition. However, if feeding on galls has a significant numerical impact on bird populations, then the birds become agents of apparent competition between the alien gallwasps and other prey outwith gallwasp communities (Holmes 1990). Both of these possibilities suggest the importance of further work on bird exploitation of invading gallwasps (see Section 6.4, Future Research). This is particularly true for alien catkin galls on Turkey oak induced by *Andricus grossulariae* and *A. quercuscalicis*, which occur at densities of up to 10^6 /tree during the May nesting season, when the link between food availability and bird reproductive success is at its strongest (van Noordwijk *et al.* 1995; Visser *et al.* 1998; Naef-Daenzer & Keller 1999; Visser *et al.* 2004).

The geographic impact of these interactions is considerable. The invading galls studied here are a subset of at least 10 species, representing 19 gall types, that have extended their distributions across Europe from native ranges south of the Alps and Carpathians to encompass a contiguous novel distribution extending northwards into Scotland and Denmark (Stone *et al.* 2002; Csóka *et al.* 2005). Areas in continental Europe have been occupied by invading gallwasps for longer (e.g. Stone & Sunnucks 1993), and I suggest that native bird populations probably exploit these aliens throughout their invaded range. The pattern of this exploitation, and the extent to which these novel resources match key phenological stages in bird life histories, will dictate the extent to which (i) invading gallwasps drive behavioural and numerical responses in bird populations; (ii) bird predation regulates alien gallwasp population dynamics; (iii) bird predation mediates indirect interactions between alien gallwasps and other prey species; and (iv) availability of these additional trophic resources prior to the breeding season ameliorates the disruptive effects of phenological mismatches between bird reproduction and native prey

attributed to global climate change (Visser *et al.* 1998; Thomas *et al.* 2001; Visser *et al.* 2003; Visser *et al.* 2004).

6.3 Changing dynamics of cynipid communities in Britain

This study has highlighted how the dynamics of communities associated with invading cynipid gallwasps in Britain change over both time and space. For the first 4 invading cynipids (*A. corruptrix*, *A. lignicolus*, *A. kollari*, *A. quercuscalicis*) previous studies have allowed direct comparison (particularly through quantitative webs) of communities associated with these first 4 invading species and how the distribution and communities associated with these established invaders have changed. In particular, changes in the distribution and community associated with the knopper (asexual) galls of *A. quercuscalicis* have now been studied intensively for over 30 years (albeit by periodic sampling for the purposes of separate studies of the population). These studies have shown the progression from early communities associated with knopper galls (Hails and Crawley, 1990), through changes in the parasitoid assemblage due to the rapid increase in inquiline cynipid abundance (Schönrogge *et al.*, 1996), a trophic group previously absent from British populations, to a phase of relatively slow recruitment of parasitoid and inquiline species, as shown in this study. This study indicates that we no longer observe a community in development, but one which may have reached a degree of stasis, perhaps for the reasons outlined in Chapter 3 (see Discussion). This conclusion cannot, however, justifiably be reached without further research, particularly including population genetic approaches (see Section 6.4, Future research).

Baseline data collected for the communities associated with the 4 more recent invading species (*A. aries*, *A. grossulariae*, *A. lucidus* and *Aphelonyx cerricola*) indicate that community development has been more rapid than recorded for *A. quercuscalicis*, particularly in the case of *A. grossulariae*. Given this accelerated rate of recruitment relative to *A. quercuscalicis*, it is difficult to predict how these communities will develop in the future. However, based on previous studies, it can be predicted that range expansion north and west across Britain will continue, and be

faster for species that already have shown more rapid range expansion (*A. aries*, *A. grossulariae*) than those with a limited distribution (*A. lucidus*, *Aphelonyx cerricola*). Possible reasons to explain the variations in the rate of expansion between species are given in Chapter 2 (see Discussion).

Quantitative webs are essential to measure the degree of apparent competition between cynipids through shared natural enemies. This study concurs with the results of Schönrogge and Crawley's study (2000) i.e. that evidence supporting the existence apparent competition between native and invading cynipids is currently weak. However, webs constructed in this study are valuable as they have revealed the breakdown of web compartments containing other gallwasp generations on the same host oaks. Breakdown of this distinction would broaden the potential for indirect interactions between gallwasp generations on the two oak groups, meriting future research (see Section 6.3 Future research).

Quantitative webs methodology in this study cannot be applied without potential sources of bias. Schönrogge and Crawley (2000) considered two of these, sampling efficiency and resolution, to be of particular importance in the system of cynipids and parasitoids. For sampling efficiency, there is a trade-off between quantification and the usefulness of food webs (Müller *et al.*, 1999). More cynipid species (15 – 20 species) were found during 4 hour searches for galls than recorded from obtaining the absolute gall densities from 2160 shoots (4 – 7 species). Rare species may therefore be missed in density samples. In assessing indirect interactions between invading and native cynipid species, it is these rare species where the asymmetric interactions may be strongest (Schönrogge and Crawley, 2000).

Resolution is also an important source of bias. Webs shown in Chapter 4 are not food webs, but instead, links represent the associations of parasitoid and inquiline species with galls rather than trophic links. Since trophic interactions within galls can be complex (Askew, 1961; Schönrogge *et al.*, 1995), parameters such as connectance are not discussed. The number of links per parasitoid species is an underestimate if they attack different hosts in the same gall. d_{ij} -values are also

overestimates because all parasitoid and inquiline emerging from host galls are treated as if they attack the cynipid larvae.

6.4 Future research

Although there have been extensive theoretical discussions, there are few field demonstrations of apparent competition between herbivorous insects (see Chapter 1 Section 1.4). During this and previous studies of cynipid quantitative webs (Schönrogge and Crawley, 2000), evidence of apparent competition was found to be weak. In the wider literature, the importance of apparent competition has been demonstrated experimentally in the marine littoral ecosystem (Schmidt, 1987; Menge, 1995) and between vertebrates mediated by pathogens (Tomkins *et al.*, 2000). In herbivorous insects, long-term apparent competition (responses over more than one generation) has been demonstrated in laboratory systems (Bonsall and Hassell, 1997) and short term apparent competition (within a generation) has been observed in aphid communities (Muller and Godfray, 1997; Morris *et al.*, 2001). Only one study successfully demonstrated the existence of long-term apparent competition using quantitative webs involved the experimental removal of two species of herbivore from a community of leaf-mining insects in a tropical forest (Morris *et al.*, 2004) (see Chapter 1, Section 1.4). In order to hypothesis test thoroughly and effectively about the existence or otherwise of apparent competition between cynipid gallwasps, manipulative experiments are very attractive, however, the suitability of the system for such experiments may be limited, given the intensity of sampling demanded, relative to that needed in other systems such as leaf-mining insects in which sample collection, management and experimental design would be far easier and more straightforward. Therefore theoretically, one could carry out such manipulative experiments, but it is my opinion that the practical considerations preclude considering manipulation of entire quantitative webs as a possibility in the cynipid gallwasp system, particularly in the course of a relatively short research program such as a PhD.

In order to progress understanding about the development of communities associated with invading gallwasps in Britain and in the invaded range continental Europe, exploration of the native recruitment hypothesis versus pursuit hypothesis is required to determine the origin of invaded parasitoids and inquilines reared from galls. In the wider literature, there is some evidence to support the native recruitment hypothesis. Recruitment of native parasitoid species by the leaf miner *Phyllocnistis citrella* (Lepidoptera: Gracillariidae) in citrus orchards in Spain occurred rapidly (Vercher *et al.*, 2005). For cynipid gallwasps, evidence to date cannot support one hypothesis over the other without population genetic techniques to provide information about the origin of community members in invaded ranges.

As alluded to above (see Section 6.2 Bird exploitation of galls), the potential effects of bird predation of galls on both alien and invading gallwasp populations suggest the importance of future work on bird exploitation of galls. By examining the pattern of exploitation of galls by birds across a longer timeframe and a wider geographic area including the invaded and native range of the cynipid galls studied, it will be possible to determine the extent to which these novel resources match key phenological stages in bird life histories and potentially affect interactions between birds and gallwasps as outlined in section 6.2. To further investigate spatial density dependence of bud gall predation by birds, several additional parameters would need to be included in analyses such as habitat features including tree density, patch quality and nest hole availability. The monitoring of bud use by birds over winter before the appearance of galls and through gall development up to bud burst would also help to identify the pattern of exploitation of galls and buds as a food resource by birds.

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Appendix

Table 7.1 Locations and grid references for all sites visited during this study

Location	Grid reference
Falkirk, Stirlingshire	NS 905786
Kelso, Roxburghshire	NT 708348
Alnwick, Cumbria	NU 173135
Gilsland, Northumberland	NY 607692
Ripon, North Yorkshire	SE 347672
Tatton, Cheshire	SJ 752813
Knebworth, Hertfordshire	TL 226213
Porthleven, Cornwall	SW 626268
Bodmin, Cornwall	SX 074667
Dawlish, Devon	SX963767
Yeovil, Somerset	ST 597168
Horsham, West Sussex	TQ 198312
Scotney, Kent	TQ 692359
Ashford, Kent	TR 000441
South Queensferry, Midlothian	NT 087788
Holyrood, Edinburgh	NT 274737
Grange, Edinburgh	NT 233712
Rosyth, Fife	NT 105839
Kincardine, Fife	NS 952876
Falkland, Fife	NO 251075
Eskine, Strathclyde	NS 453738
Kelvinside, Glasgow	NS 561675
Pollock Country Park, Glasgow	NS 562622
Falkirk, Central Region	NS 905786
Muiravonside, Central region	NS 958763
Linlithgow, West Lothian	NT 037785
Torphichen, West Lothian	NS 974722
Bathgate, West Lothian	NS 956700
Birnam, Perthshire	NO 954706
Dunkeld, Perthshire	NO 304742
Dunrobin, Golspie, Sutherland	NC848008
Beauly, Inverness-shire	NH527467
Forres, Morayshire	NJ023590
Tarskavaig, Skye	NG 591086
Armadale, Skye	NG630049
Tarbert, Argyll and Bute	NR864692
Rowardennan, Strathclyde	NN358002
Findrassie Wood, Elgin, Morayshire	NJ 200644
Ullapool, Wester Ross	NH135948
Mawgan, Lizard, Cornwall	SW711243
Idless, Truro, Cornwall	SW823479
Edney Common, Chelsford, Essex	TL660043
Regent's Park, London	TQ285825

Location	Grid reference
Coombe Bissett, Salisbury, Wiltshire	SU105283
Ruthven, Kingussie, Inverness-shire	NH692407
Castleton Village, Inverness	NH692407
Fairy Glen, Rosemarkie, Black Isle	NH728579
Newark, Nottinghamshire	SK807526
Cheltenham, Gloucestershire	SO981262
Trowbridge, Somerset	ST814599
Sittingbourne, Kent	TQ904620
Brockenhurst, Hampshire	SU280322
Windsor Great Park, Berkshire	SU964725
Ascot, Berkshire	SU931694
Richmond Park, Greater London	TQ200731
Hampstead Heath, London	TQ270867
Teignmouth, Devon	SX936752
Tiverton, Devon	SS967158
Aviemore, Inverness-shire	NH906112
Jedburgh, Roxburghshire	NT664210
Hexham, Co. Durham	NY958630
Wadebridge, Cornwall	SW985709
Bideford, Devon	SS478290
Taunton, Somerset	ST264199
Gastonbury, Somerset	ST503391
Blandford Forum, Dorset	ST868058
Winfrith Newbury, Dorset	SY810873
Maidenhead, Berkshire	SU460689
Newbury, West Berkshire	SU885215
Midhurst, West Sussex	SU885215
Goodwood, Chichester, West Sussex	SU884081
Knole Park, Sevenoaks, Kent	TQ542534
Tunbridge Wells, Kent	TQ589363
Wimbledon Common, London	TQ225709
Cirencester, Gloucestershire	SP030029
Chastleton, Oxfordshire	SP250292
Witney, Oxfordshire	SP380109
Stevenage, Hertfordshire	TL246235
Sandy, Bedfordshire	TL189481
Prestbury, Macclesfield, Cheshire	SJ895762
Peterborough, Cambridgeshire	TL147975
Grantham, Lincolnshire	SK934394
Sleaford, Lincolnshire	TF010464
Morecambe Bay, Lancashire	SD467666
Grange-over-sands, Lancashire	SD415785
Brotherton, Leeds, North Yorkshire	SE483265
Chesterfield, Derbyshire	SK408673
Thirsk, North Yorkshire	SE425825
Kendal, Cumbria	SD515951
Rockliffe, Carlisle, Cumbria	NY361626
Lockerbie, Dumfries	NY135815
Brodick, Arran, Argyll and Bute	NS008364
Ayr, Ayrshire	NS356187

Location	Grid reference
Milngavie, Strathclyde	NS558761
Callander, Stirlingshire	NN632083
Gorebridge, Midlothian	NT382634
Polbeth, West Lothian	NT040651
Melrose, Ettrick and Lauderdale	NT534330
Dirleton, East Lothian	NT506850
Gifford, East Lothian	NT535675
Crieff, Perthshire	NN876227
Guildtown, Perthshire	NO130314
Pitlochry, Perthshire	NN927582
Blair Atholl, Perthshire	NN875655
Muir of Ord, Inverness-shire	NH537507
Cawdor, Morayshire	NH848498
Poolewe, Wester Ross	NG866817

Table 7.2 Characteristics of the oak stands at the 8 sample sights across Britain (from Schönrogge *et al.*, 1998).

(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. x rosacea*.)

site numbers and names	species	<i>n</i>	trees per 100m 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
Beaully	<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

Parasitoid and gall densities from quantitative webs shown in Chapter 4. Each table relates to the corresponding web (Figures 4.1 a-f) and linkage diagrams (Figures 4.2 a-f) in Chapter 4.

Table 7.3a Parasitoid, inquiline and gall densities for quantitative web, Silwood park, spring and autumn 2005 (Chapter 4: web: Figure 4.1a, linkage diagram: Figure 4.2a)

Cynipid species	Gall density (100m ²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m ²)
Sexual generation			
<i>A. corruptrix</i>	159.62	<i>M. fuscipes</i> (p)	109.74
<i>A. grossulariae</i>	5491.21	<i>M. tibialis</i> (p)	269.18
<i>A. grossulariae</i>	5491.21	<i>M. xanthocerus</i> (p)	53.83
<i>A. grossulariae</i>	5491.21	<i>M. fuscipes</i> (p)	323.01
<i>A. grossulariae</i>	5491.21	<i>E. brunniventris</i> (p)	53.83
<i>A. grossulariae</i>	5491.21	<i>E. urozonus</i> (p)	53.83
<i>A. grossulariae</i>	5491.21	<i>T. flavipes</i> (p)	269.18
<i>A. grossulariae</i>	5491.21	<i>M. dorsalis</i> (p)	646.02
<i>A. grossulariae</i>	5491.21	<i>C. fungosa</i> (p)	161.51
<i>A. grossulariae</i>	5491.21	<i>M. amaenus</i> (p)	2960.949
<i>A. grossulariae</i>	5491.21	<i>Ormyrus. sp.</i> (p)	323.01
<i>A. kollari</i>	75.25	<i>M. fuscipes</i> (p)	50.16
<i>A. lignicolus</i>	2205.76	<i>M. fuscipes</i> (p)	1967.30
<i>A. quercuscalicis</i>	23697.56	<i>M. tibialis</i> (p)	10841.74
<i>A. quercuscalicis</i>	23697.56	<i>M. xanthocerus</i> (p)	4028.16
<i>A. quercuscalicis</i>	23697.56	<i>M. dubius</i> (p)	342.82
<i>A. quercuscalicis</i>	23697.56	<i>M. fuscipes</i> (p)	4756.65
<i>A. quercuscalicis</i>	23697.56	<i>M. sericeus</i> (p)	42.85
<i>A. curvator</i>	6.21	<i>M. tibialis</i> (p)	3.11
<i>A. curvator</i>	6.21	<i>T. flavipes</i> (p)	3.11
<i>N. quercusbaccarum</i>	4547.19	<i>M. tibialis</i> (p)	568.40
<i>N. quercusbaccarum</i>	4547.19	<i>M. fuscipes</i> (p)	63.15
<i>N. quercusbaccarum</i>	4547.19	<i>M. sericeus</i> (p)	947.33
<i>N. quercusbaccarum</i>	4547.19	<i>E. brunniventris</i> (p)	189.47
<i>N. quercusbaccarum</i>	4547.19	<i>T. flavipes</i> (p)	315.78
<i>N. quercusbaccarum</i>	4547.19	<i>M. dorsalis</i> (p)	63.15
<i>N. numismalis</i>	766.54	<i>S. radiatus/pallipes</i> (i)	766.54
<i>N. quercusbaccarum</i>	4547.19	<i>S. gallaepomiformis</i> (i)	126.31
<i>N. quercusbaccarum</i>	4547.19	<i>S. radiatus/pallipes</i> (i)	1705.20
<i>N. quercusbaccarum</i>	4547.19	<i>S. pallidipennis</i> (i)	126.31

Asexual generation			
<i>A. quercuscalicis</i>	35.44	<i>E. brunniventris (p)</i>	3.35
<i>A. quercuscalicis</i>	35.44	<i>S. biguttata (p)</i>	0.26
<i>A. quercuscalicis</i>	35.44	<i>E. urozonus (p)</i>	0.03
<i>A. quercuscalicis</i>	35.44	<i>M. dorsalis (p)</i>	0.03
<i>A. quercuscalicis</i>	35.44	<i>M. stigmatizans (p)</i>	0.06
<i>A. quercuscalicis</i>	35.44	<i>O. nitidulus (p)</i>	1.33
<i>A. quercuscalicis</i>	35.44	<i>C. fungosa (p)</i>	11.10
<i>C. longiventris</i>	38.64	<i>T. flavipes (p)</i>	15.46
<i>A. quercuscalicis</i>	35.44	<i>S. gallaepomiformis (i)</i>	18.68
<i>A. quercuscalicis</i>	35.44	<i>S. umbraculus (i)</i>	0.13
<i>N. anthracinus</i>	883.73	<i>S. gallaepomiformis (i)</i>	883.73

Table 7.3b Parasitoid, inquiline and gall densities for quantitative web, Puttenham, spring and autumn 2005 (Chapter 4: web: Figure 4.1b, linkage diagram: Figure 4.2b)

Cynipid species	Gall density (100m ²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m ²)
Sexual generation			
<i>A. corruptrix</i>	6547.29	<i>M. fuscipes</i> (p)	4364.86
<i>A. grossulariae</i>	3964.79	<i>M. tibialis</i> (p)	132.16
<i>A. grossulariae</i>	3964.79	<i>E. brunniventris</i> (p)	44.05
<i>A. grossulariae</i>	3964.79	<i>S. biguttata</i> (p)	88.11
<i>A. grossulariae</i>	3964.79	<i>T. flavipes</i> (p)	660.80
<i>A. grossulariae</i>	3964.79	<i>M. dorsalis</i> (p)	440.53
<i>A. grossulariae</i>	3964.79	<i>M. amaenus</i> (p)	2246.71
<i>A. grossulariae</i>	3964.79	<i>Ormyrus. sp.</i> (p)	44.05
<i>A. grossulariae</i>	3964.79	<i>S. variegata</i> (p)	44.05
<i>A. lignicolus</i>	8752.32	<i>M. fuscipes</i> (p)	4633.58
<i>A. quercuscalicis</i>	23936.56	<i>M. tibialis</i> (p)	4385.32
<i>A. quercuscalicis</i>	23936.56	<i>M. xanthocerus</i> (p)	1461.77
<i>A. quercuscalicis</i>	23936.56	<i>M. dubius</i> (p)	365.44
<i>A. quercuscalicis</i>	23936.56	<i>M. fuscipes</i> (p)	8587.93
<i>A. quercuscalicis</i>	23936.56	<i>C. fungosa</i> (p)	365.44
<i>A. curvator</i>	409.29	<i>T. flavipes</i> (p)	175.41
<i>A. curvator</i>	409.29	<i>M. amaenus</i> (p)	116.94
<i>N. numismalis</i>	1087.09	<i>M. tibialis</i> (p)	664.33
<i>N. numismalis</i>	1087.09	<i>M. fasciventris</i> (p)	150.98
<i>N. numismalis</i>	1087.09	<i>E. brunniventris</i> (p)	30.20
<i>N. quercusbaccarum</i>	3904.38	<i>M. tibialis</i> (p)	499.06
<i>N. quercusbaccarum</i>	3904.38	<i>M. fasciventris</i> (p)	29.36
<i>N. quercusbaccarum</i>	3904.38	<i>M. sericeus</i> (p)	733.91
<i>N. quercusbaccarum</i>	3904.38	<i>E. brunniventris</i> (p)	234.85
<i>N. quercusbaccarum</i>	3904.38	<i>T. flavipes</i> (p)	322.92
<i>N. quercusbaccarum</i>	3904.38	<i>T. geranii</i> (p)	88.07
<i>N. quercusbaccarum</i>	3904.38	<i>C. fungosa</i> (p)	88.07
<i>A. grossulariae</i>	3964.79	<i>S. gallaepomiformis</i> (i)	44.05
<i>A. curvator</i>	409.29	<i>S. radiatus/pallipes</i> (i)	116.94
<i>N. numismalis</i>	1087.09	<i>S. radiatus/pallipes</i> (i)	241.58
<i>N. quercusbaccarum</i>	3904.38	<i>S. gallaepomiformis</i> (i)	1379.74
<i>N. quercusbaccarum</i>	3904.38	<i>S. radiatus/pallipes</i> (i)	322.92
<i>N. quercusbaccarum</i>	3904.38	<i>S. pallidipennis</i> (i)	205.49

Asexual generation			
<i>A. quercuscalicis</i>	306.23	<i>E. brunniventris</i> (p)	24.07
<i>A. quercuscalicis</i>	306.23	<i>S. biguttata</i> (p)	1.50
<i>A. quercuscalicis</i>	306.23	<i>O. nitidulus</i> (p)	6.79
<i>A. quercuscalicis</i>	306.23	<i>C. fungosa</i> (p)	128.64
<i>A. quercuscalicis</i>	306.23	<i>S. gallaepomiformis</i> (i)	130.83
<i>A. quercuscalicis</i>	306.23	<i>S. umbraculus</i> (i)	2.19
<i>A. quercuscalicis</i>	306.23	<i>S. gallaepomiformis</i> (i)	0.23
<i>N. anthracinus</i>	1047.59	<i>S. gallaepomiformis</i> (i)	1047.59

Table 7.3c Parasitoid, inquiline and gall densities for quantitative web, Beaulieu, spring and autumn 2005 (Chapter 4: web: Figure 4.1c, linkage diagram: Figure 4.2c)

Cynipid species	Gall density (100m²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m²)
Sexual generation			
<i>B. pallida</i>	125.61	<i>T. flavipes</i> (p)	3.53
<i>B. pallida</i>	125.61	<i>T. geranii</i> (p)	0.67
<i>B. pallida</i>	125.61	<i>A. skianeuros</i> (p)	65.91
<i>B. pallida</i>	125.61	<i>T. cerri</i> (p)	0.17
<i>B. pallida</i>	125.61	<i>T. affinis</i> (p)	17.99
<i>N. quercusbaccarum</i>	153.00	<i>T. flavipes</i> (p)	25.50
<i>N. quercusbaccarum</i>	153.00	<i>A. skianeuros</i> (p)	76.50
<i>B. pallida</i>	125.61	<i>S. umbraculus</i> (i)	7.57
Asexual generation			
<i>A. kollari</i>	94.92	<i>T. auratus</i> (p)	31.99
<i>A. kollari</i>	94.92	<i>T. flavipes</i> (p)	1.07
<i>A. kollari</i>	94.92	<i>T. geranii</i> (p)	1.07
<i>A. kollari</i>	94.92	<i>Torymus. sp.</i> (p)	2.13
<i>A. lignicolus</i>	102.18	<i>T. auratus</i> (p)	1.23
<i>A. kollari</i>	94.92	<i>S. umbraculus</i> (i)	1.07

Table 7.3d Parasitoid, inquiline and gall densities for quantitative web, Dunrobin, spring and autumn 2005 (Chapter 4: web: Figure 4.1d, linkage diagram: Figure 4.2d)

Cynipid species	Gall density (100m ²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m ²)
Sexual generation			
<i>A. kollari</i>	117.20	<i>M. fuscipes</i> (p)	6.32
<i>A. lignicolus</i>	138.95	<i>M. fuscipes</i> (p)	6.59
<i>A. curvator</i>	3.06	<i>T. flavipes</i> (p)	2.04
<i>N. quercusbaccarum</i>	23.72	<i>M. tibialis</i> (p)	0.39
<i>N. quercusbaccarum</i>	23.72	<i>M. dubius</i> (p)	0.39
<i>N. quercusbaccarum</i>	23.72	<i>M. fuscipes</i> (p)	1.19
<i>N. quercusbaccarum</i>	23.72	<i>T. flavipes</i> (p)	14.63
Asexual generation			
<i>A. kollari</i>	0.63	<i>T. auratus</i> (p)	0.07
<i>A. lignicolus</i>	0.47	<i>T. auratus</i> (p)	0.08
<i>A. kollari</i>	0.63	<i>S. umbraculus</i> (i)	0.51

Table 7.3e Parasitoid, inquiline and gall densities for quantitative web, Silwood Park, autumn 2005 and spring 2006 (Chapter 4: web: Figure 4.1e, linkage diagram: Figure 4.2e)

Cynipid species	Gall density (100m ²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m ²)
Asexual generation			
<i>A. quercuscalicis</i>	35.44	<i>E. brunniventris</i> (p)	3.35
<i>A. quercuscalicis</i>	35.44	<i>S. biguttata</i> (p)	0.26
<i>A. quercuscalicis</i>	35.44	<i>E. urozonus</i> (p)	0.03
<i>A. quercuscalicis</i>	35.44	<i>M. dorsalis</i> (p)	0.03
<i>A. quercuscalicis</i>	35.44	<i>M. stigmatizans</i> (p)	0.06
<i>A. quercuscalicis</i>	35.44	<i>O. nitidulus</i> (p)	1.33
<i>A. quercuscalicis</i>	35.44	<i>C. fungosa</i> (p)	11.10
<i>C. longiventris</i>	38.64	<i>T. flavipes</i> (p)	15.46
<i>A. quercuscalicis</i>	35.44	<i>S. gallaepomiformis</i> (i)	18.68
<i>A. quercuscalicis</i>	35.44	<i>S. umbraculus</i> (i)	0.13
<i>N. anthracinus</i>	883.73	<i>S. gallaepomiformis</i> (i)	883.73
Sexual generation			
<i>A. corruptrix</i>	53.05	<i>M. fuscipes</i> (p)	19.89
<i>A. kollari</i>	21.23	<i>M. fuscipes</i> (p)	10.62
<i>A. lignicolus</i>	603.22	<i>M. fuscipes</i> (p)	188.51

<i>A. grossulariae</i>	288.63	<i>M. fuscipes (p)</i>	3.36
<i>A. grossulariae</i>	288.63	<i>M. dorsalis (p)</i>	6.71
<i>A. grossulariae</i>	288.63	<i>M. amaenus (p)</i>	6.71
<i>A. quercuscalicis</i>	2463.32	<i>M. tibialis (p)</i>	20.57
<i>A. quercuscalicis</i>	2463.32	<i>M. xanthocerus (p)</i>	107.58
<i>A. quercuscalicis</i>	2463.32	<i>M. dubius (p)</i>	6.33
<i>A. quercuscalicis</i>	2463.32	<i>M. fuscipes (p)</i>	109.16
<i>A. quercuscalicis</i>	2463.32	<i>C. fungosa (p)</i>	3.16
<i>A. quercuscalicis</i>	2463.32	<i>O. vernalis (p)</i>	1.58
<i>B. pallida</i>	392.81	<i>M. tibialis (p)</i>	1.60
<i>B. pallida</i>	392.81	<i>M. xanthocerus (p)</i>	0.05
<i>B. pallida</i>	392.81	<i>M. fasciiventris (p)</i>	0.05
<i>B. pallida</i>	392.81	<i>M. sericeus (p)</i>	10.03
<i>B. pallida</i>	392.81	<i>S. biguttata (p)</i>	0.72
<i>B. pallida</i>	392.81	<i>E. urozonus (p)</i>	0.05
<i>B. pallida</i>	392.81	<i>T. auratus (p)</i>	10.40
<i>B. pallida</i>	392.81	<i>T. flavipes (p)</i>	14.28
<i>B. pallida</i>	392.81	<i>T. geranii (p)</i>	1.27
<i>B. pallida</i>	392.81	<i>M. dorsalis (p)</i>	1.94
<i>B. pallida</i>	392.81	<i>O. nitidulus (p)</i>	0.33
<i>B. pallida</i>	392.81	<i>C. fungosa (p)</i>	8.30
<i>B. pallida</i>	392.81	<i>M. amaenus (p)</i>	0.77
<i>B. pallida</i>	392.81	<i>Ormyrus. sp. (p)</i>	0.39
<i>B. pallida</i>	392.81	<i>Torymus. sp. (p)</i>	22.74
<i>B. pallida</i>	392.81	<i>Pediobius. sp. (p)</i>	0.05
<i>B. pallida</i>	392.81	<i>Synergus. sp. (i)</i>	7.86

Table 7.3f Parasitoid, inquiline and gall densities for quantitative web, Puttenham, autumn 2005 and spring 2006 (Chapter 4: web: Figure 4.1f, linkage diagram: Figure 4.2f)

Cynipid species	Gall density (100m ²)	Parasitoid (p)/inquiline (i) species	Parasitoid /inquiline density (100m ²)
Asexual generation			
<i>A. quercuscalicis</i>	306.23	<i>E. brunniventris (p)</i>	24.07
<i>A. quercuscalicis</i>	306.23	<i>S. biguttata (p)</i>	1.50
<i>A. quercuscalicis</i>	306.23	<i>O. nitidulus (p)</i>	6.79
<i>A. quercuscalicis</i>	306.23	<i>C. fungosa (p)</i>	128.64
<i>A. quercuscalicis</i>	306.23	<i>S. gallaepomiformis (i)</i>	130.83
<i>A. quercuscalicis</i>	306.23	<i>S. umbraculus (i)</i>	2.19
<i>A. quercuscalicis</i>	306.23	<i>S. gallaepomiformis (i)</i>	0.23
<i>N. anthracinus</i>	1047.59	<i>S. gallaepomiformis (i)</i>	1047.59
Sexual generation			
<i>A. corruptrix</i>	758.48	<i>M. fuscipes (p)</i>	206.86
<i>A. grossulariae</i>	8306	<i>M. sericeus (p)</i>	80
<i>A. grossulariae</i>	8306	<i>C. fungosa (p)</i>	80

<i>A. grossulariae</i>	8306	<i>M. amaenus (p)</i>	80
<i>A. grossulariae</i>	8306	<i>Ormyrus. sp. (p)</i>	80
<i>A. lignicolus</i>	10666.47	<i>M. xanthocerus (p)</i>	67.08
<i>A. lignicolus</i>	10666.47	<i>M. fuscipes (p)</i>	737.93
<i>A. quercuscalicis</i>	26743	<i>M. tibialis (p)</i>	476.1
<i>A. quercuscalicis</i>	26743	<i>M. xanthocerus (p)</i>	348.88
<i>A. quercuscalicis</i>	26743	<i>M. fuscipes (p)</i>	1269.71
<i>B. pallida</i>	376.08	<i>M. tibialis (p)</i>	1.21
<i>B. pallida</i>	376.08	<i>M. xanthocerus (p)</i>	0.12
<i>B. pallida</i>	376.08	<i>M. sericeus (p)</i>	1.93
<i>B. pallida</i>	376.08	<i>S. biguttata (p)</i>	10.48
<i>B. pallida</i>	376.08	<i>E. urozonus (p)</i>	0.04
<i>B. pallida</i>	376.08	<i>T. auratus (p)</i>	4.39
<i>B. pallida</i>	376.08	<i>T. flavipes (p)</i>	7.58
<i>B. pallida</i>	376.08	<i>T. geranii (p)</i>	0.85
<i>B. pallida</i>	376.08	<i>M. dorsalis (p)</i>	0.08
<i>B. pallida</i>	376.08	<i>O. nitidulus (p)</i>	1.81
<i>B. pallida</i>	376.08	<i>C. fungosa (p)</i>	5.28
<i>B. pallida</i>	376.08	<i>C. semifascia (p)</i>	0.24
<i>B. pallida</i>	376.08	<i>M. amaenus (p)</i>	1.37
<i>B. pallida</i>	376.08	<i>Ormyrus. sp. (p)</i>	1.25
<i>B. pallida</i>	376.08	<i>Torymus. sp. (p)</i>	14.27
<i>B. pallida</i>	376.08	<i>A. skianeuros (p)</i>	0.04
<i>B. pallida</i>	376.08	<i>Synergus. sp. (i)</i>	16.41

Table 7.4 Additional records for invading gall species

Gall species	Location	Grid reference	Date
<i>A. cerricola</i>	Sand point, Somerset	ST320650	2002
<i>A. lucidus</i>	Blackhill, Hants	SU302182	2004
<i>A. grossulariae</i>	Wallington, Surrey	TQ320640	2004
<i>A. grossulariae</i>	Blackhill, Hants	SU302182	2004
<i>A. corruptrix</i>	Trooper's Hill, Bristol	ST620730	2001
<i>A. corruptrix</i>	Fritton, Norfolk	TM221998	2002