Early parasitoid recruitment in invading cynipid galls

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Summary: Biological invasions are widely seen as the biggest threat to biodiversity after the loss of habitats. One aspect of considerable interest is the recruitment of natural enemies after the establishment of the invading species and how such enemies link invaders to native communities. However, not all invaders are invasive. Eight cynipid species originating in south-eastern Europe invaded Britain over the last 200 years. Presently they cause no economic concern or have any detectable detrimental effect on the native cynipid fauna. Since their invasions have been allowed to progress without intervention, they provide an excellent opportunity to study the recruitment of natural enemies and their integration into native communities. In contrast, the invasion of Japan by *Dryocosmus kuriphilus* from China caused great economic concern, because considerable damage to its host trees, *Castanea* spp. a valuable fruit tree in Japan and elsewhere in the world, is caused at high infestation rates. Here we review the early recruitment of parasitoids to the alien species in the UK and *D. kuriphilus* in Japan, their role in the invaders population dynamics, and how they link the invaders to native cynipid communities.

Biological Invasions, Biological Control, Parasitoid Recruitment, Community Structures

Introduction

Among cynipid gall wasps there are at least three independent examples of biological invasions that have resulted from human activity. Two cases represent introductions of individual species that are significant because they affect economically important host plants. Introduced European cork oak, *Quercus suber,* in California has been colonised by a European cynipid, *Plagiotrochus suberi* (Bailey and Stange 1966), and Chestnut (*Castanea*) in Japan, North America and Europe has been colonised by *Dryocosmus kuriphilus*, a native of China and Korea (Brussino et al. 2002; Moriya et al. 1989a; Payne 1978). The most significant example of cynipid range expansion is associated with human dispersal of *Quercus cerris* in Europe. This section Cerris oak is native to Italy, the Balkans and Asia Minor, and is the host for one or both generations of a wide diversity of cynipids (Melika et al. 2000; Stone et al. 2001). The natural distributions of all European section Cerris oaks correspond closely to glacial refugia for oaks during the Pleistocene ice ages, and following the retreat of the ice sheets only oaks in the section *Quercus* (particularly *Quercus robur* and *Q. petraea*) were able to escape the refugia and recolonise northern Europe (Stone et al. 2001). As a result, no cynipids dependent on *Q. cerris* (or any other section Cerris oak) for one or both generations in their lifecycle, occur naturally in northern Europe.

Over the last 400 years *Quercus cerris* has been planted widely north and west of its native range (Stone and Sunnucks 1993), creating a mosaic of *Q. cerris* patches within the natural distribution of section *Quercus* oaks. In contrast to the situations with *D. kuriphilus* and *P. suberi* there are no geographical barriers between the native and invaded range for cynipid gall wasps using *Q. cerris.* As a result at least 10 species have subsequently invaded north-western Europe, including eight host-alternating *Andricus* species (*A. aries, A. corruptrix*, *A. gemmeus*, *A. grossulariae, A. kollari*, *A. lignicolus*, *A. lucidus* and *A. quercuscalicis*) and two species currently thought to be wholly dependent on *Q. cerris* (*Aphelonyx cerricola* and *Neuroterus saliens*)(Stone et al. 2002). *A. aries, A. corruptrix, A. grossulariae, A. lignicolus*, *A. lucidus, A. quercuscalicis* and *Aphelonyx cerricola* all reached Britain between 1950 and 2000, 2000km from the nearest natural *Q. cerris* stands, apparently without direct human assistance. *Andricus kollari* has spread naturally across most of northern Europe, but was also deliberately introduced into Britain from the eastern Mediterranean in the first half of the nineteenth century (Askew 1984; Stone et al. 2001). Range expanding cynipids have proven to be valuable model systems for studies on the recruitment of communities of natural enemies (Stone and Schönrogge 2003; Stone et al. 2002).

We first review the studies on parasitoid recruitment to the galls of *Andricus quercuscalicis,* the most extensively studied species in Europe. Secondly we consider the invasions of *A. corruptrix, A. kollari, A. lignicolus,* and *A. quercuscalicis* and how parasitoid species link the aliens to the native cynipid community, asking why these communities are invasible. Lastly, we will draw on evidence from these gallwasp invasions including that of *D. kuriphilus* in Japan to assess the role of parasitoid recruitment in the invasion process.

Parasitoid recruitment to the galls of *Andricus quercuscalicis*

Andricus quercuscalicis is a host-alternating invader in Western Europe (described above), establishing populations along a 2000km invasion route from the Balkans to Britain (Schönrogge et al. 1995). First records outside the native range date as far back as 1631 from the southeast of Germany. Since then the species was described from the area of Berlin in 1787, and Bejerinck in the Netherlands described its life-cycle and the switch from *Q. cerris* to *Q. robur* between generations in 1882 (Schönrogge 1994 and therein). Claridge (1962) first recorded the species in Britain in 1958 and in 1986 the galls were first recorded from Ireland (Schönrogge 1994 and therein). These and some additional natural historic records provide a rough timeline of the spread of *A. quercuscalicis* across Europe. With the above dates and data on the parasitoid assemblage richness from the asexual galls from sites along the invasion route, it is possible to estimate the residence time of *A. quercuscalicis* in the regions described by Schönrogge et al. (1995). A simple regression of residence time against the residuals of a log-log regression of species richness against sample size (correcting for variable sample sizes) explains 91% of the variability in parasitoids species richness across the invaded range ($F_{1,3}=30.5$, $p<0.05$). Thus parasitoid species richness is increasing with residence time and, possibly more significantly, the parasitoid assemblages associated with the asexual galls of *A. quercuscalicis* in the invaded range were subsets of those known from the native range (Schönrogge et al. 1995).

After *A. quercuscalicis* arrived in Britain the galls of the asexual generation remained virtually parasitoid free for about 20 years. Despite extensive rearings the first parasitoid records (*Torymus cyanaeus* and *Mesopolobus amaenus*) were only obtained in the late 1970's. *T. cyanaeus* has never been reared again from *A. quercuscalicis*, while *M. amaenus* attacked inquilines soon after their appearance in *A. quercuscalicis* galls, but has since remained rare. In this regard it seems to represent an early successional species in community development in the U.K. Curiously, though native to europe this parasitoid has not been found in rearing of galls from the European continent (Hails et al. 1990; Schönrogge et al. 1995). Other opportunistic parasitoid species included ichneumonid parasitoids, *Mastrus castaneus* and *Gelis formicarius*, and the diapriid *Spilomicrus stigmaticalis* (Hails et al. 1990). The only inquiline species recorded during the 1980s was *Synergus pallicornis* and attack rates for both inquilines and parasitoids were generally low (<10%). However, subsequent recruitment of species such as *M. sericeus*, *Sycophila biguttata, Eupelmus urozonus* represents the addition of taxa a. known to attack hosts inside cynipid galls, b. later found to attack hosts in the asexual galls of *A. quercuscalicis* in its native range, but c. were all part of the native British parasitoid fauna (Askew 1961; Hails et al. 1990; Schönrogge et al. 1995).

Between 1990 and 1995 there was a sharp increase in the abundance of some parasitoid species and others were recorded for the first time. Both were closely associated with the recruitment of inquiline *Synergus*, and particularly *Synergus gallaepomiformis*, to the asexual galls of *A. quercuscalicis* in the south-east of Britain. Both the geographical pattern of inquiline infestation and parasitoid recruitment followed the invasion route of the host (Schönrogge et al. 1996). Thus the recruitment process observed across Europe was mirrored on a smaller scale within Britain. The fact that parasitoid assemblages in the invaded range were almost perfect subsets of those recorded from the native range leaves in our view two non-exclusive hypotheses: (a) The recruited parasitoid species are from the native community and are pre-adapted to exploit the new host at the species level (native recruitment hypothesis), or (b) the parasitoid species attacking the host in its invaded range are “strains” that have pursued the host from the native range and represent invading genotypes (pursuit hypothesis).

Recruitment of parasitoid species to sexual generation galls of *A. quercuscalicis* was similar to that of the asexual galls in that assemblies recorded from Britain represented a subset of those recorded from the continent (Stone et al. 1995). However, we are not aware of time lags between the arrival in a new range and the recruitment of parasitoids to this generation. This is perhaps surprising, since the sexual generation galls are formed on an introduced tree, *Q. cerris*, but all the parasitoid species attacking these galls also attack the sexual generation galls of *Andricus kollari* which arrived and spread throughout Britain 100 years before *A. quercuscalicis*. Thus a shift in the host searching behaviour of the parasitoid species between tree species could have happened even before *A. quercuscalicis* was in the country.

The convergence of the parasitoid faunas in the invaded and native ranges, despite differing environmental conditions and resident cynipid faunas, suggests a strong link between gall attributes (including host tree species, phenology, the plant organ galled, gall morphologies) and parasitoid community composition, species richness and abundance.

The galls induced by the two generations of *A. quercuscalicis* differ in several respects. The sexual generation gall is thin walled, 1–2 mm long, and develops very rapidly on the catkins of *Quercus cerris*. In contrast, the asexual generation gall has a thick woody wall, reaches a diameter of up to 20mm, and develops over several months on the acorns of *Q. robur*. These differences have two major consequences for the associated communities: (*a*) 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). In contrast, the rapid development of the sexual generation galls prevents such temporal structuring of parasitoid attack. (*b*) The asexual generation galls are attacked by several inquiline *Synergus* species, but the far smaller sexual generation galls never harbour inquilines, perhaps because they develop too rapidly to allow the development of secondary inquiline larval chambers. Despite the major differences in host gall properties, in its native range the two generations of *A. quercuscalicis* support equally rich assemblages: 12 species in the sexual generation (all parasitoids) and 13 in the asexual generation (10 parasitoids, 3 inquilines). However, in the asexual generation only 4 of the 10 parasitoids feed predominantly on the gall wasp larva (the rest attacking inquilines), whereas in the sexual generation all of the parasitoid species attack the gall wasp or other parasitoids (Schönrogge et al. 1995; Stone et al. 1995). Only a single parasitoid is common to the communities of both generations, but plays a different role in each. In the sexual generation gall, the parasitoid *Cecidostiba fungosa* attacks the gall wasp larva. In the asexual generation this parasitoid attacks only inquilines in the outer wall of the gall, probably because at the time *C. fungosa* attacks, the gall wasp larva is beyond the reach of its short ovipositor. A final difference between the two communities is that across the range of *A. quercuscalicis* the mortality inflicted by parasitoid attack is far higher in the sexual generation (20–49%) than in the asexual generation (5–15%) (Hails and Crawley 1991, 1992; Schönrogge et al. 1995; Stone et al. 1995). Although the reasons for this difference are probably complex, it is tempting to suggest that the thin-walled, sexual generation galls are more vulnerable to attack by a rich assemblage of small parasitoids with short-ovipositors than the asexual generation galls. The differences in size and phenology between the galls induced by the two generations of *A. quercuscalicis* are shared with other cynipid species (Melika et al. 2000) and although detailed studies of the parasitoid assemblages associated with both generations of a cynipid species are rare (Askew 1961, 1980), strong differences between host generations are probably a common feature of oak cynipid communities.

Invaded cynipid communities in Britain

Indirect interactions through having shared natural enemies, and in particular through apparent competition (Holt 1977), are thought to be common and strong among endophytic insects because the sessile life style during their larval stages makes direct competitive interactions less likely. Yet indirect interactions through the food plant have also been reported (Sitch et al. 1988; Whitham 1978).

Eight communities of cynipid galls in Britain were studied intensively in 1994 and 1995 that included 1 – 4 of four alien species (*Andricus corruptrix*, *A. kollari*, *A. lignicolus*, and *A. quercuscalicis*) (Schönrogge et al. 1998, 2000). However, although Schönrogge and Crawley (2000) used equivalent methods to those applied in similar studies on aphid and leafminer systems in which apparent competition appeared to play a major role (Morris et al. 2004; Müller et al. 1999), they found no indication that apparent competition was important in shaping cynipid communities. They observed strong impacts of the aliens on the parasitoid populations, i.e. host shifts, changes in population sex-ratios and, in one community, satiation effects where host densities alternated between years and parasitoid abundance appeared to be limited by the low host densities (Schönrogge and Crawley 2000; Schönrogge et al. 1999), yet the indirect interactions among hosts were always weak.

The analysis of the quantified webs established for the eight communities also indicated that locally the parasitoid species appeared much more specialized than their species status as generalists would suggest. Where parasitoid species were shared among hosts, with few exceptions (e.g. *Eupelmus urozonus*, *Eurytoma brunniventris*), more than 90% of adults emerged from only one type of gall and generally less than 5% from any single alternative host. Based on current data it is not possible to distinguish whether local specialization is genetically fixed or whether host switches occur. However, it has been suggested that increased host fidelity promotes the stability of host – parasitoid communities that include generalist parasitoid species (Hastings and Godfray 1999).

The main feature of all eight communities studied by Schönrogge and Crawley (2000) is the isolation of the parasitoid assemblages associated with the galls of the sexual generations of the alien species on *Q. cerris*. These assemblages include four pteromalid species, *Mesopolobus dubius, M. fuscipes, M. tibialis* and *M. xanthocerus*. With the exception of *M. tibialis* (and probably *M. dubius*) the species are univoltine and only a few individuals of *M. tibialis* were reared from galls other than those on *Q. cerris*. As a consequence, there is no parasitoid species that is shared between any native cynipid and any of the invaders that would link those through both generations, but with shared natural enemy attack in only alternate generations, apparent competition would not be expected to occur.

We would suggest that this isolation and the degree of specialization within local parasitoid populations allow the coexistence of such a species rich fauna. Also the local community structure of galls and parasitoids determines part of the niche space into which an invading species may fit.

However, the absence of a tight linkage between the population dynamics of hosts and parasitoids does not mean that parasitoid attack can not affect the host populations. With attack rates sometimes found to be higher than 90%, they do affect gall densities and species that share parasitoid attack, such as the sexual generations of the alien species on *Q. cerris*, are likely to affect each others mortality rates within that generation. However, other sources of mortality such as bird predation that shows a more density dependent pattern of attack on this same set of galls (Schönrogge et al. 1999) are more likely to exert a degree of population regulation or even control.

Parasitoid recruitment by *Dryocosmus kuriphilus* in Japan

Dryocosmus kuriphilus is a univoltine cynipid gall wasp that induces galls on chestnut trees, *Castanea* spp. After its accidental introduction from China to Japan in 1941 (Shiraga 1951) it spread rapidly and was recorded by the late 1950s throughout the range of its host trees (Moriya et al. 2002). During a study from 1978 to 1981 at the Fruit Tree Research Station at Yatabe, Japan, 10 species of parasitoids were recorded from the invasive galls and 5 of them were reared regularly between years (Otake et al. 1982). All but one of the 10 species are thought to have more than one generation each year, which means that their population dynamics were not closely tight to *D. kuriphilus* and they were not expected to exert any population control on the invading gall wasp. *Torymus beneficus* is univoltine and it phenology was reasonably matched with *D. kuriphilus* yet by 1981 *D. kuriphilus* populations remained uncontrolled. In 1982 a closely related parasitoid species from China, *T. sinensis*, was released and within 5 years the galling rate per chestnut shoot decreased spectacularly from about 43% to only 3%. Since the tolerable injury level was estimated at 30% (Gyoutoku and Uemura 1985; Moriya et al. 1989b), this represents economic control of the pest.

Like *T. beneficus*, *T. sinensis* is univoltine and its phenology well synchronized with *D. kuriphilus* and it is not clear why one species has very little effect on the host population, while the other is a more efficient control agent. Two features in the parasitoids biology have been suggested to explain the difference. Although *T. beneficus* seems to be univoltine, precise phenology data showed the occurrence of two emergence peaks (referred to as early and late emergence peaks) separated by 4 weeks during a year. In contrast, *T. sinensis* emerges in one emergence period between the two emergence peaks of *T. beneficus* and appears to be better synchronized with *D. kuriphilus*. This very fine phenological difference (1 – 2 weeks) may explain the higher efficiency of *T. sinensis* to control *D. kuriphilus* populations (Moriya et al., 1989a). Another explanation lies in the fact that *T. beneficus* has a shorter ovipositor than *T. sinensis*. *T. beneficus* does in fact attack only relatively small galls i.e. the galls can outgrow the parasitoid, and so represent a refuge from attack, while *T. sinensis* can overcome this defense mechanism and attack larger galls. (Otake 1980; Otake et al. 1982).

Since the invasions of Japan, *D. kuriphilus* has invaded the United States and Europe. Details of these later invasions and prospects of *D. kuriphilus* in Europe are discussed elsewhere in this book.

Summary

Both the alien species in Britain and *D. kuriphilus* in Japan recruited largely multivoltine generalist parasitoids and at least for the asexual galls of *A. quercuscalicis* in Britain there was a considerable time lag (about 20 years) until a consistent parasitoid assemblage was established. While univoltine parasitoid species are rarer within the assemblages, where they occur they appear to have shifted hosts almost entirely to the alien species. This is true for the three *Mesopolobus* species that attack the sexual galls of *A. quercuscalicis* and *T. beneficus* attacking *D. kuriphilus*. As a consequence the parasitoid assemblages associated with the sexual galls of *A. quercuscalicis* and the other species that make galls on *Quercus cerris* studied today are isolated from those of native species. The apparent lack of tightly coupled host-parasitoid pairings is one aspect that allows the coexistence of cynipids in species rich communities and is one aspect that makes native cynipid communities invasible. Also, the differences between *T. sinensis* and *T. beneficus* in their biologies and the impact they have on *D. kuriphilus* population dynamics, demonstrates that host-parasitoid dynamics need to be finely tuned for the parasitoid to exert population control.

Literature

Askew, R.R. (1961) On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Transactions of the Society for British Entomology, 14, 237-268.

Askew, R.R. (1980) The diversity of insect communities in leaf-mines and plant galls. Journal of Animal Ecology, 49, 817-829.

Askew, R.R. (1984). The biology of gall- wasps. In The biology of galling insects (ed T.N. Anathakrishnan), pp. 223-271. Oxford and IBH publishing CO., New Dehli.

Bailey, S.F. and Stange, L.A. (1966) The twig wasp of cork oak. Journal of Economic Entomology, 59, 663 - 668.

Brussino, G., Bosio, G., Baudino, M., Giordano, R., Ramello, F., and Melika, G. (2002) Il cinipide galligeno *Dryocosmus kuriphilus* Yasumatsu: un pericoloso insetto esotico per il castagno europeo. L'Informatore Agrario, 37, 59 - 61.

Claridge, M.F. (1962) *Andricus quercuscalicis* (Burgsdorf) in Britain. The Entomologist, 95, 60 - 61.

Gyoutoku, Y. and Uemura, M. (1985) Ecology and biological control of the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) 1. Damage and parasitization in Kumamoto Prefecture. Proceedings of the Association for Plant Protection of Kyushu, 31, 213 - 215.

Hails, R.S. and Crawley, M.J. (1991) The population dynamics of an alien insect: Andricus quercuscalicis (Hymenoptera: Cynipidae). Journal of Animal Ecology, 60, 545-562.

Hails, R.S. and Crawley, M.J. (1992) Spatial density dependence in populations of a cynipid gall- former Andricus quercuscalicis. Journal of Animal Ecology, 61, 567-584.

Hails, R.S., Askew, R.R., and Notton, D.G. (1990) The Parasitoids and inquilines of the agamic generation of *Andricus quercuscalicis* (Hym.; Cynipidae) in Britain. The Entomologist, 109, 165-172.

Hastings, A. and Godfray, H.C.J. (1999) Learning, host fidelity, and the stability of host-parasitoid communities. American Naturalist, 153, 295-301.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology, 12, 197-229.

Melika, G., Csoka, G., and Pujade-Villar, J. (2000) Check-list of oak gall wasps of Hungay, with some taxonomic notes (Hymenoptera: Cynipidae, Cynipinae, Cynipini). Annales Historico Naturales Musei Nationalis Hungarici, 92, 265-296.

Moriya, S., Inoue, K., and Mabuchi, M. (1989a) The use of Torymus Sinensis to control chestnut gall- wasp, Dryocosmus kuriphilus, in Japan. Technical Bulletin of the Food and Fertilizer Technology Center, 118, 1-12.

Moriya, S., Inoue, K., Otake, A., Shiga, M., and Mabuchi, M. (1989b) Decline of the chestnut gall- wasp population, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) after the establishment of Torymus sinensis Kamijo (Hymenoptera: Torymidae). Applied Entomological Zoology, 24, 231-233.

Moriya, S., Shiga, M., and Adachi, I. (2002) Classical biological Control of the chestnut gall wasp in Japan. In Proceedings of the 1st International Symposium on Biological Control of Arthropods (ed R.G.v. Driesche), pp. 407- 415 United States Department of Agriculture, Forest Service, Washington, USA.

Morris, R.J., Lewis, O.T., and Godfray, H.C.J. (2004) Experimental evidence for apparent competition in a tropical forest food web. Nature, 428, 310-313.

Müller, C.B., Adriaanse, I.C.T., Belshaw, R., and Godfray, H.C.J. (1999) The structure of an aphid-parasitoid community. Journal of Animal Ecology, 68, 346-370.

Otake, A. (1980) Chestnut gall- wasp, Dryocosmus kuriphilus Yasumatsu (Hymenoptera: Cynipidae): a preliminary study on trend of adult emergence and some other Ecological aspects related to the final stage of its life cycle. Applied Entomological Zoology, 15, 96-105.

Otake, A., Shiga, M., and Moriya, S. (1982) A study on parasitism of the chestnut gall- wasp, Dryocosmus kuriphilus Yasumatsu (Hymenoptera: Cynipidae) by Parasitoids indigenous to Japan. The Bulletin of the fruit tree research station, a, 177-192.

Payne, J.A. (1978). Oriental chestnut gall- wasp: new nut pest in north America. In Proceeding of the American chestnut Symposium (eds W.L. Macdonald, f.C. Cech, J. Luchok and C. Smith), pp. 86-88. West Virginia University, Morgantown.

Schönrogge, K. (1994) Dynamics of the guild structure in the parasitoids and inquilines of an alien gall wasp, *Andricus quercuscalicis* Burgsdorf, pp. 1 - 126. Unpublished PhD Thesis, Imperial College University of London.

Schönrogge, K. and Crawley, M.J. (2000) Quantitative webs as a means of assessing the impact of alien insects. Journal of Animal Ecology, 69, 841-868.

Schönrogge, K., Stone, G.N., and Crawley, M.J. (1995) Spatial and temporal variation in guild structure - parasitoids and inquilines of *Andricus quercuscalicis* (Hymenoptera, Cynipidae) in its native and alien ranges. Oikos, 72, 51-60.

Schönrogge, K., Stone, G.N., and Crawley, M.J. (1996) Alien herbivores and native parasitoids: Rapid development of guild structure in an invading gall wasp *Andricus quercuscalicis* (Hymenoptera: Cynipidae). Ecological Entomology, 21, 71-80.

Schönrogge, K., Walker, P., and Crawley, M.J. (1998) Invaders on the move: parasitism in the sexual galls of four alien gall wasps in Britain (Hymenoptera

: Cynipidae). Proceedings of the Royal Society of London Series B-Biological Sciences, 265, 1643-1650.

Schönrogge, K., Walker, P., and Crawley, M.J. (1999) Complex life cycles in Andricus kollari (Hymenoptera, Cynipidae) and their impact on associated parasitoid and inquiline species. Oikos, 84, 293-301.

Schönrogge, K., Walker, P., and Crawley, M.J. (2000) Parasitoid and inquiline attack in the galls of four alien, cynipid gall wasps: host switches and the effect on parasitoid sex ratios. Ecological Entomology, 25, 208-219.

Shiraga, T. 1951. Problems and control of the chestnut gall wasp. *Nogyô oyobi Engei (Agriculture and Horticulture)* 26: 167-170

Sitch, T.A., Grewcock, D.A., and Gilbert, F.S. (1988) Factors affecting components of the fitness in a gall-making wasp (*Cynips divisa* Hartig). Oecologia, 76, 371-375.

Stone, G.N. and Schönrogge, K. (2003) The adaptive significance of insect gall morphology. Trends in Ecology and Evolution, 18, 512-522.

Stone, G.N. and Sunnucks, P. (1993) Genetic Consequences of an Invasion through a Patchy Environment - the Cynipid Gallwasp *Andricus quercuscalicis* (Hymenoptera, Cynipidae). Molecular Ecology, 2, 251-268.

Stone, G., Atkinson, R., Rokas, A., Csoka, G., and Nieves-Aldrey, J.L. (2001) Differential success in northwards range expansion between ecotypes of the marble gallwasp Andricus kollari: a tale of two lifecycles. Molecular Ecology, 10, 761-778.

Stone, G.N., Schönrogge, K., Atkinson, R.J., Bellido, D., and Pujade-Villar, J. (2002) The population biology of oak gall wasps (Hymenoptera: Cynipidae). Annual Review of Entomology, 47, 633 - 668.

Stone, G.N., Schönrogge, K., Crawley, M.J., and Fraser, S. (1995) Geographic and between generation variation in the parasitoid communities associated with an invading gallwasp, *Andricus quercuscalicis* (Hymenoptera:Cynipidae). Oecologia, 104, 207-217.

Whitham, T.G. (1978) Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. Ecology, 59, 1164-1176.