Parasitoid recruitment to the globally invasive chestnut gall wasp *Dryocosmus kuriphilus*

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Summary: The chestnut gall wasp *Dryocosmus kuriphilus* is a global pest of chestnut (*Castanea*). Established as a pest in the mid 20th century in Japan, Korea and the USA, this species has now reached Europe. Successful deployment of a biocontrol agent, *Torymus sinensis*, in Japan has led to its early release in Italy. Here we provide the first overview of the natural enemies associated with *D. kuriphilus* in its native and invaded ranges, and discuss general patterns in community development. We then use what is known about European oak gall wasp communities to predict possible future developments for *D. kuriphilus*, and possible interactions between parasitoid communities attacking hosts on chestnut and oaks.

Key words: Biological Invasions, Biological Control, Parasitoid Recruitment, Community Structure, *Dryocosmus kuriphilus*

Introduction

Because of human transportation, non-native species have become integral components of many ecosystems worldwide, threatening ecosystem integrity, biodiversity, agriculture and human health. Understanding the causes and consequences of biological invasions (invasion biology) represents an increasingly important challenge for ecologists and evolutionary biologists. The chestnut gall wasp (CGW), *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera, Cynipidae), is the most important global insect pest of chestnut (*Castanea spp*., Fagaceae) (Brussino et al. 2002; Moriya 1990; Murakami et al. 1995; Payne 1983). This gall wasp is a member of the tribe Cynipini, most of which induce galls on oaks *Quercus*) and is the only member of this tribe to attack chestnut (Stone et al. 2002).

Attack by the CGW attack reduces fruit yield by 50-75% (Payne 1983), and heavy attack reduces tree vigor and wood production (Kato and Hijii 1997) and can kill the tree (Moriya et al. 2002). Frequent exchange of cultivars between chestnut growers and a parthenogenetic reproductive strategy (Nohara 1956) have made *D. kuriphilus* a successful invader in Asia, North America and Europe. Japan was the first region invaded by the CGW, and here the promise of future biological control was demonstrated by successful reduction of CGW populations using an introduced Chinese parasitoid, *Torymus sinensis*. *T. sinensis* has just been released in an attempt to control the most recent CGW invasion, in Italy, representing the first recorded establishment of this pest in Europe.

Preliminary surveys of the natural enemies attacking the CGW in Italy show that it is already attacked by a suite of chalcid parasitoids characteristic of native European oak cynipid gall wasp communities on oak (reviewed in Stone *et al*. 2002). Overlap in the natural enemies attacking the invader and native communities raises the possibility of natural biological control, and of impacts on native faunas of introduction of *T. sinensis*. Here we review the global history of invasion and recruitment of natural enemies to *D. kuriphilus*, and discuss possible future development of the community centered on *D. kuriphilus* in Europe.

The invasion history of *D. kuriphilus*

The CGW emerged as a pest in the mid-twentieth century. Although first formally recorded from Japan in 1958 (Murakami et al. 1980), outbreaks in China in 1941 and 1959 suggest that the CGW is native to this region (Moriya et al. 1990; Murakami et al. 1980). The first country invaded was Japan, where the CGW was accidentally introduced to Okayama prefecture around 1940 (Oho and Umeya 1975). It spread throughout Japan within 25 years, with a dramatic impact on chestnut production (Oho and Shimura 1970; Shirakami 1951). CGW was then reported from Chaenchun, Chungchungpuk-do, Korea in 1958 (Cho and Lee 1963), over 37 years spread across South Korea (Murakami et al. 1995). In 1974, CGW colonized the American continent, and was first reported in Peach County, Georgia (Payne et al. 1976). By 1976, it had already spread to 3 adjacent counties (Houston, Crawford and Bibb). Despite a severe impact on the chestnut industry, no further information was found in the literature. CGW was first recorded from Europe in 2002, in Piemonte, Italy (Brussino et al. 2002). Once recognised, the galls were recorded at 6 localities (Boves, Peveragno, Chiusa Pesio, Borgo San Dalmazzo, Roccavione and Robilante) over an area of 160 square km. This leads us to believe that the actual introduction date is 1995-1996, when eight Chinese chestnut cultivars were introduced to the region. By 2005, the CGW had reached five new Italian regions (Lazio, Campania, Toscana, Abruzzo and Marche) covering a major part of the peninsula, and was recorded for the first time in neighboring regions of France (Val de Blore and Isola) (G Bosio and J-C Malausa 2005 personal communication) and Slovenia.

The natural enemies of *D. kuriphilus* in China, and initiation of biological control in Japan

Over the sixty-five years following its introduction to Japan (Murakami et al. 1980), scientists have achieved biological control of CGW and left an extensive literature on its invasion biology. After its arrival around 1940 and rapid spread, initial control attempts using chemical pesticides were frustrated by protection of the immature stages within the gall (Murakami 1981; Torii 1959). Subsequent breeding of resistant chestnut varieties enabled chestnut growers to control the CGW for about 20 years, until the appearance of a strain of *D. kuriphilus* able to attack resistant chestnut varieties (around 1960).

The finding that *D. kuriphilus* did not seem to have a serious impact on chestnut trees in its native China suggested that populations there were held at low densities by natural enemies (Murakami et al. 1980). A total of 11 species in 4 chalcid families (Torymidae, Ormyridae, Eurytomidae and Eupelmidae) are known from the native range of *D. kuriphilus* (see table 1). In 1975, a delegation of the Japanese Ministry of Agriculture and Forestry was sent to China to investigate the potential for biological control of

D. kuriphilus in Japan. 69 CGW galls were collected in Hsi-an, Shensi and imported to Japan, where 8 parasitoid species were reared (table 1) (Murakami 1980). In 1981, Murakami added *Eurytoma setigera* and *Megastigmus nipponicus*, and Luo and Huang (1993) added *Sycophila* (=*Decatoma*) *concinna*. A striking feature of the *D. kuriphilus* community, discussed further below, is the absence of cynipid inquilines - a major component of the communities associate with most oak cynipid galls (Stone et al. 2002).

Table 1. CGW parasitoid community in its native range (China). Species sampled from the original 69-gall rearing are marked with an asterisk (*). Key to references: 1= Murakami et al. (1980), 2= Murakami (1981), 3= Luo and Huang (1993), 4= Kamijo (1981)

Parasitoid species	**Family**	**References**
Eupelmus urozonus *	Eupelmidae	1,2
Eurytoma brunniventris *	Eurytomidae	1,2
Eurytoma setigera	Eurytomidae	2
Megastigmus maculipennis *	Torymidae	1,2
Megastigmus nipponicus	Torymidae	2
Ormyrus pomaceus (= *O. punctiger*) *	Ormyridae	1,2
Sycophila concinna	Eurytomidae	3
Sycophila variegata *	Eurytomidae	1,2
Tetrastichus sp. *	Eulophidae	1,2
Torymus geranii *	Torymidae	1,2
Torymus sinensis *	Torymidae	1,2,4

Of these, only *Torymus sinensis* (named by Kamijo in 1982) showed high host specificity and a life cycle matching that of its host – traits required for a successful biological control agent. In 1979 and 1981, approximately 5000 CGW galls were imported from China and in 1982, 260 mated *T. sinensis* females were released onto Japanese chestnut trees at the Fruit Tree Research Station (FTRS) in Ibaraki prefecture (Ôtake et al. 1984). A study carried on in 1983 showed that *T. sinensis* was successfully attacking the local target host population (Moriya et al 1990). There were some initial failures in establishment of *T. sinensis*. Research at Kumamoto Fruit Tree Experiment Station (Kumamoto Prefecture) using a third CGW shipment from China showed that establishment of *T. sinensis* was slowed by both mortality inflicted by facultative hyperparasitoids and a low female sex ratio (Murakami and Gyoutoku, 1991, 1995; Murakami and Kiyota 1983; Murakami et al. 1985, 1989, 2001).

Nevertheless, the *T. sinensis* population at the FTRS grew by a factor of 25 times by 1989 (Moriya et al. 1990), becoming the commonest parasitoid reared from CGW at FTRS. *T. sinensis* was reared from target galls more than 12 Km from its release point, showing good dispersal ability. Importantly for the chestnut industry, the proportion of chestnut shoots infested with CGW galls decreased rapidly from a maximum of 40% in 1983 to 3% in 1988 (Moriya et al. 1990), well below the estimated tolerable injury level of 30% (Guoutoku and Uemura 1985).

Parasitoids attacking *Dryocosmus kuriphilus* in Japan

Table 2. Parasitoids attacking *Dryocosmus kuriphilus* in Japan. Species recorded in China are named in **bold**. §= Species associated with Japanese oak gall wasps. Key to references: 1= Yasumatsu (1955), 2= Kamijo (1981), 3= Alam (1994), 4= Murakami et al. (1994), 5= Yasumatsu and Kamijo (1979), 6= Murakami and Gyoutoku (1995), 7= Ôtake et al. (1982), 8= Ôtake (1989), 9= Murakami et al. (1977), 10= Kato and Hijii (1999), 11= Toda et al. (2000), 12= Murakami et al. (1993), 13= Watanabe (1957)

Parasitoid species	Family	References
Chalcids		
Amblymerus sp.	Pteromalidae	1
Arthrolytus usubai§	Pteromalidae	2
Caenacis peroni§	Pteromalidae	2
Cecidostiba fushica§	Pteromalidae	2
Cecidostiba semifascia§	Pteromalidae	2
Cynipencyrtus flavus§	Encyrtidae	3, 4, 5
Cynipencyrtus sp.	Encyrtidae	6
Eupelmus urozonus	Eupelmidae	3, 4, 5, 6, 7, 8
Eupelmus sp.	Eupelmidae	7
Eurytoma brunniventris	Eurytomidae	1,3, 4, 5, 6, 7, 8, 9
Eurytoma schaeferi§	Eurytomidae	5
Eurytoma setigera	Eurytomidae	4, 5, 6, 7
Megastigmus maculipennis	Torymidae	1, 3, 4, 5, 6
Megastigmus nipponicus§	Torymidae	3, 4, 5, 6, 8; 10
Mesopolobus yasumatsui§	Pteromalidae	2, 3, 6
Ormyrus flavitibialis§	Ormyridae	4, 5, 6, 7, 8
Ormyrus pomaceus (= *O. punctiger*)	Ormyridae	1, 4, 5, 7, 8
Pteromalus apantelophagus§	Pteromalidae	2, 7
Sycophila variegata	Eurytomidae	1, 3, 4, 5, 6
Tetrastichus sp.	Eulophidae	3, 4, 6
Torymus beneficus§	Torymidae	4, 5, 6, 7, 8, 10, 11
Torymus geranii	Torymidae	1, 4, 5, 6, 7, 8
Torymus sinensis (native)	Torymidae	12
Non-chalcid parasitoids		
Aspilota yasumatsui	Braconidae	13
Cynipid inquiline		
Synergus sp.	Cynipidae	7

In Japan *D. kuriphilus* is now attacked by a rich parasitoid assemblage (table 2) of 26 chalcid species in 7 families and 1 braconid (*Aspilota yasumatsui*). Its galls have also been colonized by a cynipid inquiline *Synergus sp*. A striking feature of this community is its high richness compared to data from the Chinese native range of *Dryocosmus kuriphilus*, and the latter is almost certainly understudied. The 20 parasitoids identified to species in Japan can be divided into 10 shared with the Chinese community and 10 absent in China but recorded in Japan.

Ten of the 11 parasitoids attacking CGW in China also attack it in Japan, raising the possibility that parasitoids, as well as the gall-inducer, were introduced from China. Of the 10 shared species, 8 are known to attack native Japanese oak gall wasps (Kamijo 1981; Yasumatsu and Kamijo 1979), and for these species both introduction and shifts from native hosts are possible. However, one parasitoid (*Tetrastichus sp*.) was never recorded in Japan prior to introduction of *D. kuriphilus* (Murakami 1981) and now has no known alternative Japanese host. This species may have been imported with the chestnut gall wasp around 1940, or have recruited from an unknown Japanese host. *T. sinensis* was recorded from Tsushima Island, Japan, by Murakami et al. (1993). However, this population differs in adult emergence phenology from wasps imported from China and is thought to be native to Japan. No host other than *D. kuriphilus* is yes known for this strain of *T. sinensis*. This situation may parallel that seen in *T. sinensis* in Korea (see below).

Ten parasitoid species associated with Japanese oak gall wasps also attack CGW (table 2), representing host shifts from natives to the invader. *T. beneficus* is particularly interesting because it exists as two phenologically distinct ecotypes in galls of *D. kuriphilus*. At least two strains an “early-season strain" and a ”late-season strain”, can be differentiated based on the period of adult emergence (Murakami 1988; Ôtake 1987). It is thought that these strains represent ecotypes of the same species attacking different native cynipid hosts prior to the arrival of CGW (Murakami 1988). *T. beneficus* also illustrates another form of interaction between native cynipid communities and *D. kuriphilus*, through its formation of fertile hybrids with introduced *T. sinensis* (Moriya et al. 1992, 2002). Individuals morphologically intermediate between *Torymus sinensis* and *T. beneficus* appeared in the field (Moriya et al. 1992; Yara et al. 2000), and their hybrid origin proven using molecular markers (Izawa et al. 1992; 1995; 1996; Toda et al. 2000; Yara, 2004; 2006; Yara et al. 2000).

The abundance of literature records allows us to examine the recruitment history of parasitoids on *D. kuriphilus* in Japan. For data published between 1978 and 1993 there is no simple pattern of community enrichment over time, as might be expected. Most of the species in table 2 were present in most of the samples collected over this period (Alam 1994; Murakami 1994; Murakami and Gyoutoku 1995; Ôtake et al. 1982, Yasumatsu and Kamijo 1979). The only exceptions are four pteromalids (*Arthrolytus usubai, Caenacis peronni, Cecidostiba fushica, C. semifascia* and *Pteromalus apanthelophagus*) that were only recorded in 1981, suggesting that these records represent opportunistic and eventually unsuccessful host shifts early in the invasion process. Overall, data from Japan suggest that 38 years after its introduction, the parasitoid community associated with *D. kuriphilus* has stabilized, after a rapid early recruitment unrecorded in the literature.

Japan is the only region in which any cynipid inquiline has been reared from galls of *D. kuriphilus*. Only a single female *Synergus* sp. was reared (Ôtake et al. 1982), emphasizing the extreme rarity of inquilines in this gall.

Parasitoids attacking *D. kuriphilus* in Korea

Table 3. Parasitoids attacking *D. kuriphilus* in Korea. Species recorded from *D. kuriphilus* in China are named in **bold**. Key to references: 1= Kamijo (1981), 2= Murakami et al. (1994), 3= Murakami et al. (1995), 4= Murakami and Gyoutoku (1995), 5= Ôtake (1989), 6= Kim (1998), 7= Yasumatsu and Kamijo (1979), 8= Ko (1971), 9= Kamijo (1982), 10= Murakami et al. (1985)

Parasitoid species	Family	References
Caenacis peroni	Pteromalidae	1
Eupelmus sp.	Eupelmidae	2, 3, 4, 5, 6
Eupelmus urozonus	Eupelmidae	3, 6, 7
Eurytoma brunniventris	Eurytomidae	3, 6, 7
Eurytoma setigera	Eurytomidae	3, 6
Megastigmus maculipennis	Torymidae	6, 7
Megastigmus nipponicus	Torymidae	6, 7
Mesopolobus yasumatsui	Pteromalidae	1
Ormyrus flavitibialis	Ormyridae	6, 7
Ormyrus pomaceus (=*O. punctiger*)	Ormyridae	3, 6, 7
Sycophila variegata	Eurytomidae	3, 6, 7, 8
Torymus geranii	Torymidae	3, 6, 7
Torymus koreanus	Torymidae	9
Torymus sinensis[1]	Torymidae	6, 10
Torymus sp.	Torymidae	6

1. Note that *T. sinensis* in Korea exists in two phenologically distinct strains (see main text).

After its arrival in Korea, *D. kuriphilus* recruited a rich parasitoid assemblage of 15 chalcid species (table 3).

This community shows substantial overlap with those recorded in China and Japan. All but 6 (including 2 undescribed species) of the parasitoids recorded from Korea were recorded from China, and so may represent host shifts from native Korean hosts. Of this group of 4 species, all but one (*T. koreanus*) were among the parasitoid recruited in Japan. The lower richness in Korea compared to Japan is hard to interpret: it may be a product of the more recent arrival (by *circa* 20 years) of the invading host in Korea, or an artifact of sampling effort.

Although *Torymus sinensis* was never imported to Korea, this species was recorded by Murakami et al. (1995) throughout the country. Based on differences in adult emergence phenology, Korean populations were described as a different strain to those in China (Murakami et al. 1993). Furthermore, in a manner paralleling the observations for *T. beneficus* in Japan, Korean *T. sinensis* were further subdivided into two strains (the KA and the G-3 populations) on the basis differences in adult emergence phenology and exploitation of different native oak cynipid hosts before the CGW invasion (Murakami et al. 1995).

Parasitoids attacking *D. kuriphilus* in the USA

Despite a dramatic impact of the CGW on the chestnut industry in the USA, very little has been published on its natural enemies. Only two torymid species, *Torymus advenus* and *T. tubicola* (Payne 1978) are recorded.

Parasitoids attacking *D. kuriphilus* in Italy

Galls of *D. kuriphilus* were reared to census natural enemy recruitment immediately after its discovery, in 2003, 2004 and 2005. Fifteen chalcid parasitoid species belonging to six families were recorded (see table 4).

Of the parasitoids found in Italy, four are shared with the communities reared in China, Korea and Japan. While it is possible that these species were introduced with the Chinese *D. kuriphilus*, the cultivars introduced in Italy in 1995-1996 carried no dried galls, suggesting that CGW was probably present in buds as eggs or first instar larvae. These hosts were probably too young to have been attacked by these parasitoids. In fact, all of the species in Table 4 are well known as parasitoids of oak cynipid hosts in

Europe, and many of them (see table 4) are widespread in the Western Palaearctic. The remainder are characteristic of oak cynipid communities in southern and mediterranean Europe. All of these parasitoid records almost certainly represent recruitment from local cynipid communities.

Early recording of parasitoid communities in Italy captured the rapid recruitment process inferred also to have occurred in Japan. Community richness rose from 4 species in 2002, to 7 in 2003, 10 in 2004 and 14 in 2005 (Table 4). Despite the increase in community richness, gall attack rates (estimated per inhabitant) have remained very low: from 1.6% in 2003 (n=1900 galls), to 0.8% in 2004 (n=2500) and 0.5% in 2005 (n=6713 galls). Of the parasitoids attacking *D. kuriphilus* in Italy, the most significant and consistent is *Eupelmus urozonus* (Table 4).

Table 4. Parasitoids attacking *D. kuriphilus* in Italy, with date of first record (Date), geographic distribution in the Western Palaearctic (Dist: WP= western palaearctic, M= Southern and mediterranean Europe), and the proportion of parasitism made up by each species in Italian rearings in 2003, 2004 and 2005. Abundance estimates were unavailable (*) for *B. pallidae* and *O. pomaceus*. Species also attacking *D. kuriphilus* in China Korea and Japan are named in **bold**

Parasitoid species	Family	Date	Dist	2003	2004	2005
Sycophila iracemae	Eurytomidae	2004	M		4	
Sycophila variegata	Eurytomidae	2003	WP	2		
Sycophila biguttata	Eurytomidae	2005	WP			3
Eurytoma pistacina	Eurytomidae	2004	M		1	8
Eurytoma brunniventris	Eurytomidae	2002	WP		2	
Mesopolobus mediterraneus	Pteromalidae	2004	M		1	1
Mesopolobus sericeus	Pteromalidae	2003	WP	5		
Mesopolobus tarsatus	Pteromalidae	2005	M			1
Torymus auratus	Torymidae	2005	WP			1
Torymus flavipes	Torymidae	2003	WP	2	5	1
Torymus scutellaris	Torymidae	2005	WP			1
Megastigmus dorsalis	Torymidae	2002	WP	14		7
Eupelmus urozonus	Eupelmidae	2002	WP	77	87	77
Baryscapus pallidae	Eulophidae	2005	M	*	*	*
Ormyrus pomaceus	Ormyridae	2002	WP	*	*	*

Initiation of biological control of *D. kuriphilus* in Italy

Following successful use of *T. sinensis* to control the CGW in Japan, in 2003 Italian entomologists conducted preliminary tests to investigate efficacy of this parasitoid in Italy. For these trials, 80 pairs of Japan-sourced *T. sinensis* were released on young infested chestnut trees in outdoor net cages. Because of a discrepancy between adult parasitoid emergence and gall development, the females were not able to successfully attack *D. kuriphilus*. In 2004, while further experiment were conducted in outdoor net cages, 55 pairs of *T. sinensis* were sleeved over CGW-infested shoots in 4 localities. Again, phenological mismatch largely prevented successful attack and only 2 adult parasitoids emerged from the sleeved experiments. In 2005, the development of CGW galls shipped from Japan was delayed by cooling, allowing artificial synchronization of *T. sinensis* emergence with gall development. Ninety mated females were released in the field in three localities, in ongoing trials.

Common patterns in the development of *D. kuriphilus* communities

Communities associated with *D. kuriphilus* show consistent patterns worldwide – with the exception of North America, where the community is clearly under-studied.

1. The parasitoids attacking CGW show strong overlap with those attacking oak cynipid gall wasps locally.

2. The parasitoids shared with oak cynipids are dominated by species with a broad host range – a feature epitomized by the pan-Palaearctic species *Eurytoma brunniventris*, *Eupelmus urozonus*, *Ormyrus pomaceus* and *Sycophila variegata*. These are among the most cosmopolitan of all parasitoids found in cynipid galls (Stone *et al.* 2002, Csóka et al 2005), and *E. urozonus* even attacks inquiline cynipids in galls induced by cecidosid moths on *Rhus* in South Africa (van Noort *et al.* 2006). This pattern is extended in local parasitoid faunas: in Italy, the species attacking *D. kuriphilus* include almost all of the parasitoids known to attack cynipid hosts on at least two of oaks, sycamores and roses (*Baryscapus pallidae, Eurytoma pistacina, Mesopolobus sericeus, Sycophila biguttata, S. iracemae* and *Torymus flavipes*) (Stone *et al.* 2002, Csóka et al 2005, Schönrogge and Askew 2006). This suggests that ability to exploit a diversity of plant environments is associated with rapid detection and exploitation of *D. kuriphilus* in its invaded range.

3. The interaction between parasitoid communities centered on native and invading cynipid hosts covers a broad parasitoid taxonomic spectrum. In Italy, for example, *D. kuriphilus* is already attacked by members of all 6 of

the parasitoid families attacking native oak cynipids (Stone et al. 2002, Csóka et al. 2005).
4. The time lag between arrival of the invader and development of a community is very short. This implies that the novel gall morphology of *D. kuriphilus* and its development on a novel plant host (this species is the only Cynipid to develop on *Castanea* worldwide) are not significant barriers to its detection and exploitation by parasitoids normally resident on oaks, *Quercus*.
5. Even endoparasitoids characteristic of oak cynipids are able rapidly to exploit *D. kuriphilus*. *Sycophila biguttata* is a known endoparasitoid (Stone *et al*. 2002), and the same is probably true for *S. iracemae* and *S. variegata*. This highlights the fact that though *D. kuriphilus* has a unique ecology among the Cynipini, it is phylogenetically nested within them (Liljeblad 2002) and so, once discovered, is probably physiologically exploitable by many oak cynipid parasitoids.
6. As elsewhere, inquiline cynipids are extremely rare in *D. kuriphilus* galls in Europe. As phytophages, these inquilines may be more sensitive to the divergent host exploited by *D. kuriphilus*.

Future development of the community associated with *D. kuriphilus* in Europe.

There are two native chestnut species in Europe: *Castanea sativa* is native to Turkey, Greece and the southern Balkans, perhaps also native in Italy, and planted throughout Europe as far north as Britain. *Castanea crenata* is native to Italy, Spain and Portugal. The combined native and planted ranges of these species cover much of the temperate Western Palaearctic, and define the potential scope of range expansion by *D. kuriphilus*. Europe has seen a wave of gall wasp invasions associated with human dispersal of Turkey oak, *Q. cerris* in which multiple species have escaped southern glacial refugia and expanded their distributions north as far as Scotland (Stone *et al*. 2002). In principle, *D. kuriphilus* could invade, interact with native parasitoids and, via them, native cynipids over a similar range. The same applies to *Torymus sinensis*, if it becomes established in Italy.

From an ecological perspective, *D. kuriphilus* represents an experiment (albeit unwanted) in the recruitment of natural enemies, and in the changing mortality these inflict on the host. In comparison with the invading oak cynipids, *D. kuriphilus* is recruiting natural enemies rather rapidly (see Schönrogge et al, this volume; Stone et al. 2002). For example, the asexual generation galls of the invader *Andricus quercuscalicis* in Britain were free of parasitoids and inquilines for about 20 years (Schönrogge et al. 2000). The high rate of recruitment in Italy may reflect in part the high diversity of parasitoids (60+ species) attacking oak cynipids in southern central Europe (Schönrogge and Askew 2006). The extensive information available on the host ranges of European oak cynipids makes it possible to identify the following Europe-native parasitoids as possible future recruits to the community centered on *D. kuriphilus*. All are polyphagous and recorded from large, woody oak cynipid galls (Schönrogge and Askew 2006): *Torymus geranii* (Torymidae, already known to attack the CGW in China, Japan and Korea), *Ormyrus nitidulus* (Ormyridae), *Caenacis lauta*, *Cecidostiba semifascia* (already known to attack the CGW in Japan), *Cecidostiba fungosa, Mesopolobus amaenus, Cyrtoptyx robustus* (all Pteromalidae), *Eupelmus annulatus* (Eupelmidae) and *Baryscapus berhidanus* (Eulophidae)

A key issue in development of the CGW community is whether or not cynipid inquilines are recruited. These represent additional hosts for parasitoids and have a significant positive impact on parasitoid community richness (Schönrogge et al. 1994, 1996, this volume). However, it remains to be seen whether native European cynipid inquilines will be able to exploit galls induced on *Castanea*. The unique position of *Dryocosmus kuriphilus* as a chestnut galler among cynipid gall inducers suggests that this host shift is not an easy one.

Invading European *Andricus* gall wasps also experienced an increase over time in the mortality inflicted by natural enemies, reaching more than 40% in their sexual generation galls (e.g. Schönrogge et al 1994, 1996, 2000, Schönrogge et al., this volume). A qualitatively similar response is to be expected for *D. kuriphilus*, particularly if this host becomes abundant relative to oak cynipids. Female lineages within parasitoid species able to locate the novel host and with appropriate phenology are then expected to achieve high reproductive success, and so spread through parasitoid populations. This in turn may result in the development of genetically discrete *D. kuriphilus* ecotypes within parasitoid species (Stone and Schönrogge 2003). A potential candidate for this pattern already reared from *D. kuriphilus* is *Torymus scutellaris*, a member of the *Torymus erucarum* species group, which, like *T. sinensis* and *T. beneficus* are typically univoltine and show close phenological matching to their host (see also Schönrogge et al. this volume). Increasing attack rates are also expected to reduce the high between-year variation in community composition evident in Table 4. The basis for predictions of this type would be much improved by further work on the biodiversity and population genetic structure of parasitoid communities of oak and chestnut cynipids throughout the native and introduced range of *D. kuriphilus*.

Impacts of *D. kuriphilus* on native European cynipid communities

The high local abundance achieved by *D. kuriphilus* in Italy suggests that, once discovered, this host may represent a significant resource for parasitoids. By exploiting galling sites on an otherwise unexploited plant host, *D. kuriphilus* avoids possible competition for oviposition sites with native cynipids (Stone et al. 2002) and has the potential to massively elevate local host (and hence parasitoid) populations. The rapid recruitment of generalist parasitoids shared with oak cynipids suggests that *D. kuriphilus* may have a negative impact on native cynipids through apparent competition (Holt 1977, Schönrogge et al. this volume). Whether this effect materializes depends on the extent to which parasitoids show a positive density dependent response to increasing *D. kuriphilus* density and distribution, and on levels of parasitoid population flow between chestnuts and oaks. These key issues require detailed quantitative monitoring of parasitoid populations on native hosts and on *D. kuriphilus*, ideally using quantified web approaches (e.g. Schönrogge and Crawley 2000), and the deployment of genetic approaches to analyze parasitoid population structure (Hayward and Stone 2006, Yara et al. 2000, Yara 2004, 2006).

Finally, release of *T. sinensis* could have a range of potential impacts. If this parasitoid can successfully track the phenology of CGW in Europe, it has the potential to act as a control agent (Schönrogge et al, this volume). Its high specificity to *D. kuriphilus* to date suggests that it has limited potential for exploitation of native hosts, but enforced changes in phenology may mean that extrapolation from experience elsewhere is unreliable. As *T. sinensis* populations evolve, so probably will their host range. Finally, the possibility remains of interaction with native torymids through hybridization. These possibilities again call for detailed monitoring of the communities associated with both native cynipids and *D. kuriphilus*.

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