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A. Quacchia, C. Ferracini, J.A. Nicholls, E. Piazza, M.A. Saladini, F. Tota, G.  
Melika, A. Alma

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**Chalcid parasitoid community associated with the invading pest *Dryocosmus kuriphilus* in north-western Italy**

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3 1 **Chalcid parasitoid community associated with the invading pest *Dryocosmus kuriphilus* in**  
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5 2 **north-western Italy**  
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10 4 Running title: Native parasitoids of *Dryocosmus kuriphilus*  
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15 6 Ambra Quacchia<sup>1</sup>, Chiara Ferracini<sup>1</sup>, James A. Nicholls<sup>2</sup>, Enzo Piazza<sup>1</sup>, Matteo Alessandro  
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17 7 Saladini<sup>1</sup>, Federica Tota<sup>1</sup>, George Melika<sup>3</sup>, Alberto Alma<sup>1</sup>  
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22 9 <sup>1</sup>DIVAPRA-Entomologia e Zoologia applicate all' Ambiente 'Carlo Vidano', University of Turin,  
23  
24 10 Grugliasco (TO), Italy  
25

26  
27 11 <sup>2</sup>Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK  
28

29 12 <sup>3</sup>Pest Diagnostic Laboratory, Vas County Plant Protection and Soil Conservation Directorate,  
30  
31 13 Tanakajd, Hungary  
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34 14  
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36 15 Correspondence: Ambra Quacchia, DIVAPRA-Entomologia e Zoologia applicate all' Ambiente  
37  
38 16 'Carlo Vidano', University of Turin, via Leonardo da Vinci 44, 10095, Grugliasco (TO), Italy.  
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41 17 Phone number: 00390116708677, Fax: 00390116708535, E-mail: ambra.quacchia@unito.it  
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**Abstract**

1. Biological invasions of exotic species pose a major threat to native biodiversity. Invaders are known to have direct impacts on native species; however, less well studied are the indirect impacts mediated through the integration of invaders into trophically-linked communities.

2. A survey of the chalcid wasp parasitoid community attacking the chestnut gallwasp *Dryocosmus kuriphilus* was carried out over a five year period at 26 sites in north-western Italy. More than 415,000 galls were collected and more than 10,000 parasitoid specimens emerged. Twenty-seven parasitoid species belonging to six families (Eurytomidae, Pteromalidae, Torymidae, Eupelmidae, Ormyridae, Eulophidae) were identified using morphological and molecular methods; seventeen are new records for the parasitoid community associated with *D. kuriphilus* in Italy. The morpho-species complexes *Megastigmus dorsalis*, *Eupelmus urozonus*, *E. annulatus* and *Eurytoma pistaciae* were the dominant species, another six morpho-species were encountered regularly but at low frequency, and 13 species were recorded only occasionally. The attack rate of any individual parasitoid species was low, although the more common species appeared to be increasing their use of this novel host.

3. Biases observed in the sex ratios of parasitoids emerging from *D. kuriphilus* galls suggest that parasitoid individuals are making life history decisions to take advantage of the high abundance of this host. Overall, these patterns imply that there is ongoing transfer of parasitoids between oak and chestnut galls, and hence a high potential for this invading species to have a major impact on native oak gall communities via indirect competition mediated through shared parasitoids.

**Keywords**

*Dryocosmus kuriphilus*, Chalcidoidea, indigenous parasitoids, biodiversity, chestnut gallwasp

## 51 Introduction

52 The introduction of exotic species is occurring more and more frequently around the world,  
53 especially in countries with extensive international exchange of goods and tourists, and poses a  
54 widely recognized threat to native biodiversity (Williamson, 1996; Wittenberg & Cock, 2001).  
55 Understanding the causes and consequences of biological invasions subsequent to such  
56 introductions represents an increasingly important challenge for ecologists and evolutionary  
57 biologists. Many invasive species undergo population explosions and spread rapidly since they are  
58 released from their normal controls of disease and natural enemies (van Lenteren *et al.*, 2006). The  
59 resulting ecological impact of invaders can occur at different levels of biological organisation from  
60 genetic effects through effects on individuals, populations or communities to effects on ecosystem  
61 processes (Parker *et al.*, 1999). Expanding populations of exotic species can disrupt ecosystems  
62 directly through displacement and extinction of native species (Wilson, 1997), causing both  
63 economic and environmental damage. Invasive herbivores may affect populations and communities  
64 of native herbivores by competing for the same resource, although mechanisms underlying  
65 competition are not always fully understood (Reitz & Trumble, 2002). However, when trophic links  
66 are established between invasive species and native communities, invaders can impact indirectly on  
67 these communities through perturbed trophic structures (Vitousek *et al.*, 1996; Hennemann &  
68 Memmot, 2001). Hence understanding the process by which native natural enemies recruitment  
69 onto novel invading hosts provides insight into the broader effects of invading species.

70 *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera, Cynipidae), native to China, is a key pest  
71 of chestnut trees (Fagaceae, *Castanea* spp.) (Payne *et al.*, 1983; Moriya *et al.*, 1990; Murakami *et*  
72 *al.*, 1995). This species became established in the mid 20<sup>th</sup> century in Japan, Korea and the USA. In  
73 Europe it was first reported in 2002 from Piedmont in north-west Italy (Brussino *et al.*, 2002), but  
74 from customs records its introduction can be traced back to 2–3 years beforehand with the  
75 importation of nursery material from China (Quacchia *et al.*, 2008). Due to the severe impact that  
76 the galls induced by this species have on host plant growth and nut production it was added to the

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3 77 European Plant Protection Organization (EPPO) A2 Action list (EPPO, 2005) in 2003. *Dryocosmus*  
4  
5 78 *kuriphilus* has one generation per year, with parthenogenetic females laying eggs in the buds of  
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7  
8 79 *Castanea* spp. during summer which then hatch in 30-40 days. First instar larvae overwinter and  
9  
10 80 grow slowly until the following spring at which point their growth rate increases leading to the  
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12 81 induction of galls inside which the gallwasp larvae develop. Native parasitoids that normally attack  
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15 82 galls induced by related cynipid gallwasps on oaks (Fagaceae, *Quercus* spp.) have colonised *D.*  
16  
17 83 *kuriphilus* galls everywhere throughout their introduced range (Aebi *et al.*, 2006, 2007). Given the  
18  
19 84 high abundance of *D. kuriphilus* galls, the use of this species as a host by oak gall parasitoids may  
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21 85 have massive, but to date unstudied, impacts on the oak gall community through the process of  
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23 86 apparent competition (Holt, 1977). However, to understand the impacts of this invading species we  
24  
25 87 first need to know basic information on the identity and behaviour of native parasitoids colonising  
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27 88 it.

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30  
31 89 A total of 11 species in five chalcid families (Torymidae, Ormyridae, Eurytomidae,  
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33 90 Eupelmidae and Eulophidae) are known to attack *D. kuriphilus* in its native range in China  
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35 91 (Murakami *et al.*, 1980; Kamijo, 1981; Murakami, 1981; Luo & Huang, 1993). Of these, only  
36  
37 92 *Torymus sinensis* Kamijo, shows high host specificity and a life cycle matching that of its host; the  
38  
39 93 remaining species also attack related cynipid hosts galling oaks. In Japan introduced *D. kuriphilus* is  
40  
41 94 now attacked by a rich parasitoid wasp assemblage of 24 chalcid species from seven families and  
42  
43 95 one braconid species (*Aspilota yasumatsui* Watanabe) (Aebi *et al.*, 2006; Abe *et al.*, 2007). After its  
44  
45 96 arrival in Korea, *D. kuriphilus* recruited a parasitoid assemblage of 17 chalcid species over a period  
46  
47 97 of only several decades (Ko, 1971; Yasumatsu & Kamijo, 1979; Kamijo, 1981, 1982; Murakami *et*  
48  
49 98 *al.*, 1985, 1994, 1995; Ôtake, 1989; Ôtake *et al.*, 1982; Kim, 1998). Preliminary surveys of the  
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51 99 natural enemies attacking *D. kuriphilus* in Italy were published by Aebi *et al.* (2006, 2007) in which  
52  
53 100 15 species belonging to five chalcid families were identified. Although the communities associated  
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55 101 with introduced populations of *D. kuriphilus* are richer than those found in its native Chinese range,  
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57 102 the latter is almost certainly understudied. However, the parasitoid communities of *D. kuriphilus* in

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3 103 both native and introduced ranges show substantial overlap in species composition and consistent  
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5 104 biological patterns (Aebi *et al.*, 2006). Parasitoid communities based around invading *D. kuriphilus*  
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8 105 develop rapidly, involving species shared with local populations of oak gallwasps, typically those  
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10 106 with broad host ranges. The novel communities are also diverse, both taxonomically and in terms of  
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12  
13 107 the life histories of component species. Although the recruitment of indigenous parasitoids onto  
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15 108 invading populations of *D. kuriphilus* has been fast, they have not yet provided effective control of  
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17 109 this pest. Given the severity of the damage caused by *D. kuriphilus* and the failure of other methods  
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19  
20 110 of control (such as insecticides or selection of resistant cultivars), control by native parasitoids has  
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22 111 been augmented by the release of *T. sinensis*, initially into Japan (with rapid effective control;  
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24  
25 112 Moriya *et al.*, 1990) and subsequently to both the USA (Cooper & Rieske, 2007; Rieske, 2007) and  
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27 113 Italy (Quacchia *et al.*, 2008).

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29 114 Here we present a detailed report on the native natural enemies associated with *D. kuriphilus*  
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32 115 in the north of Italy where *D. kuriphilus* was first introduced. We provide a qualitative assessment  
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34 116 of the species utilising *D. kuriphilus* as a host to examine how the parasitoid community has  
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36 117 changed over the past five years since the preliminary surveys of Aebi *et al.* (2006). We also  
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38  
39 118 provide quantitative data to examine the rate of parasitoid recruitment onto this novel host, and to  
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41 119 examine how the demographics of this novel abundant host may affect life history decisions of the  
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44 120 parasitoids attacking it. Finally we discuss the possible future development of the *D. kuriphilus*  
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46 121 parasitoid community and its interaction with the parasitoid community attacking hosts on oaks.  
47

## 48 122 **Materials and methods**

### 49 50 123 *Gall collection and rearing*

51  
52  
53 124 Parasitoids were reared from galls of *D. kuriphilus* collected during the years 2006-2010.  
54  
55 125 Galls were collected from 26 sites within Cuneo province in north-western Italy, within a zone of  
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57  
58 126 850 km<sup>2</sup> bounded by 44°38'52'' and 44°12'05'' N and by 7°19'19'' and 7°49'21'' E (Figure 1).  
59  
60 127 This area has extensive infestation by *D. kuriphilus* and encompasses its initial introduction site into  
128 Italy, so likely contains the most species-rich parasitoid assemblage available. Sampled chestnut



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3 129 trees were located both in mixed forests and in chestnut orchards; Cuneo province has 40% of its  
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6 130 forestry area covered by chestnut and nearly 10% by *Quercus* spp. (IPLA, 2004). Galls were  
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8 131 randomly collected by hand from low branches and with the aid of lopping shears from the  
9  
10 132 medium-high canopy. All material was stored in plastic bags, transferred to a forest nursery  
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13 133 “Gambarello” at Chiusa Pesio within Cuneo province and separated from any non-gall plant  
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15 134 material to avoid contamination by other insects not associated with the galls. Galls were collected  
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17 135 twice a year: in winter withered galls formed during the previous spring were sampled, and in  
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20 136 summer newly formed galls were collected. The dried winter galls were kept in cardboard boxes  
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22 137 provided with extractable skylights while the fresh summer galls were isolated inside Plexiglas and  
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24  
25 138 net cubes (40x40x40 cm). In both cases multiple galls (up to 2,000) were kept in every container.  
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27 139 All galls were stored outdoors at ambient conditions.  
28

#### 29 140 *Parasitoid collection and identification*

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31  
32 141 Rearing boxes were checked once per week until the emergence of the first parasitoid wasp,  
33  
34 142 after which parasitoids were collected daily and their date of emergence recorded. Gall-inducing  
35  
36 143 and parasitoid wasps were removed using an entomological pooter, then stored in 99% ethanol. All  
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38  
39 144 the parasitoids were initially identified using morphological characters. Voucher specimens of  
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41 145 parasitoids were deposited at the University of Turin, DIVAPRA Entomology section. Some of the  
42  
43 146 parasitoid taxa encountered contain morphologically-cryptic species distinguishable only through  
44  
45  
46 147 the use of molecular markers; these groups include *Megastigmus dorsalis* (Fabricius), *Eurytoma*  
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48 148 *brunniventris* Ratzeburg and the *Eupelmus urozonus* Dalman/*E. annulatus* Nees complex  
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50  
51 149 (Kartinen *et al.*, 2010; Nicholls *et al.*, 2010). Between 7 and 43 individuals per morpho-species  
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53 150 complex were sequenced to determine whether multiple species were present. The sample for each  
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55 151 morpho-species was derived evenly from the winter and summer collections of their hosts. Samples  
56  
57  
58 152 were sequenced either for the cytochrome *b* gene (*Megastigmus*, *Eurytoma*) following methods in  
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60 153 Nicholls *et al.* (2010) or the cytochrome oxidase I gene (*Eupelmus*) following Kartinen *et al.*  
154 (2010). These molecular methods were only used for a qualitative assessment of the presence of

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3 155 cryptic species to provide a comprehensive picture of the species diversity attacking *D. kuriphilus*.

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5 156 As resources were not available for molecular identification of every parasitoid specimen all the  
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8 157 quantitative analyses of abundance described below were performed at the level of morpho-species  
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10 158 rather than genetic species.

#### 11 12 13 159 *Abundance patterns in the parasitoid community*

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15 160 The number of emerged adults of each parasitoid species was counted and a standardised  
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17 161 emergence rate was calculated by dividing the number of emerged adults by the number of galls  
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20 162 sampled in that collecting period. Since *D. kuriphilus* galls are multilocular, multiple parasitoids of  
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22 163 the same species could emerge from the same gall; our rearing method meant we were unable to  
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24  
25 164 determine if this was the case. Hence our emergence rate is not a measure of the exact rate of  
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27 165 parasitism, but does provide a method of determining relative parasitoid abundance per unit of  
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29 166 sampling effort. Changes over time in the emergence rate of each species in each season were tested  
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31  
32 167 for using a logistic regression implemented in SPSS version 17.0. Dates of emergence of the 4 most  
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34 168 common parasitoid morpho-species from galls collected in 2009 were plotted to assess whether  
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36 169 emergence (and hence parasitism of new hosts) coincided with the development of the next  
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39 170 generation of host galls. The secondary sex ratios (i.e. the sex ratio of emerging adults) for each of  
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41 171 these 4 species in each season were tested against the null hypothesis of a 50:50 sex ratio, using a  $\chi^2$   
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43  
44 172 goodness-of-fit test to examine whether they showed a similar bias to that seen in parasitoids  
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46 173 attacking other invading cynipid hosts.

## 47 48 174 **Results**

### 49 50 51 175 *Parasitoid species emerging from galls*

52  
53 176 In total 415,224 galls were collected (371,855 withered winter galls and 43,369 newly formed  
54  
55 177 spring galls; Table 1). A total of 10,077 native parasitoid specimens from the superfamily  
56  
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58 178 Chalcidoidea emerged across five years. Twenty-three species in six chalcid families (Eurytomidae,  
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60 179 Pteromalidae, Torymidae, Eupelmidae, Ormyridae, Eulophidae) were identified using  
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morphological characters (Table 2). The molecular analyses revealed the presence of cryptic species

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3 181 within all of the morpho-species complexes tested, thus adding a further 4 species to the list of  
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6 182 parasitoids attacking *D. kuriphilus*. Both cryptic species recognised by Nicholls *et al.* (2010) were  
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8 183 found within the *M. dorsalis* morpho-species, although one was sampled at much higher frequency  
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10 184 (all but one of the 43 individuals screened). The presence of *E. bruniventris* was confirmed, but  
11  
12 185 some individuals provisionally identified as this species were in fact *Eurytoma adleriae* Zerova.  
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14  
15 186 Individuals assigned to the morpho-species *Eupelmus urozonus* were found to be either *E. urozonus*  
16  
17 187 or *E. fulvipes* Förster, and individuals identified morphologically as *Eupelmus annulatus* were either  
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19  
20 188 *E. annulatus* or *E. spongipartus* Förster.  
21

22 189 Some parasitoid species were found to attack *D. kuriphilus* galls only occasionally, with  
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25 190 fewer than ten specimens in total recorded sporadically across the survey period. This was the case  
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27 191 for *Aulogymnus arsames* (Walker), *Baryscapus* sp., *Pediobius chilaspidis* Bouček, *P. saulius*  
28  
29 192 (Walker), *Pediobius* sp., *Eupelmus splendens* Giraud, *Ormyrus pomaceus* (Geoffroy), *O. nitidulus*  
30  
31 193 (Fabricius), *Cecidostiba* sp., *Mesopolobus amaenus* (Walker), *M. tarsatus* (Nees), *M. tibialis*  
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33 194 (Westwood) and *Torymus flavipes* (Walker). Other species were found more consistently with  
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35  
36 195 records from the majority of years, but were only present at low frequency. This set of species  
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39 196 included *Sycophila variegata* (Curtis), *S. biguttata* (Swederus), *E. bruniventris*, *Mesopolobus*  
40  
41 197 *sericeus* (Förster), *Aulogymnus* sp. and *Aprostocetus* sp. (Table S1). Some of these species appeared  
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43 198 to be increasing in abundance over time, and often were absent in the early years of sampling, so  
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45  
46 199 our data may reflect the initial colonisation of *D. kuriphilus* by these species.  
47

48 200 Finally, four species were recorded every year at high frequency: *M. dorsalis*, *E. urozonus*, *E.*  
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50 201 *annulatus* and *Eurytoma pistaciae* Rondani (Table S1). The most frequently collected species was  
51  
52  
53 202 *M. dorsalis*. Overall, this morpho-species accounted for 33.3% of all parasitoid emergences during  
54  
55 203 the study, followed by *E. pistaciae*, *E. annulatus* and *E. urozonus* with 30.1%, 14.1%, and 14.0%,  
56  
57  
58 204 respectively. Three of these species, *M. dorsalis*, *E. annulatus* and *E. pistaciae*, showed significant  
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60 205 increases in emergence rate from overwintering galls over the sampling period ( $R^2=0.938$ ,  $P=$   
206  $0.007$ ;  $R^2=0.930$ ,  $P=0.008$ ;  $R^2=0.790$ ,  $P=0.044$  respectively). Neither overwintering *E. urozonus*

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3 207 nor any species emerging from galls collected in summer showed significant increases in  
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6 208 emergence rate over time (Figure 2). All four species showed an emergence pattern consisting of  
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8 209 two generations per year (Figure 3). The first generation overwintered in *D. kuriphilus* galls and  
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10 210 emerged from the end of April until early June. The second generation resulted from attack of  
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12 211 developing galls, with emergence beginning at the end of June and continuing until the end of July  
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14  
15 212 or early August (Figure 3). Of these four common parasitoid morphospecies, *M. dorsalis*,  
16  
17 213 *Eupelmus urozonus* and *E. annulatus* showed a general pattern of strongly male-biased sex ratios in  
18  
19 214 their overwintering generations and weakly female-biased ratios in the generations developing  
20  
21 215 within freshly growing *D. kuriphilus* galls (Table 3). The fourth species, *E. pistaciae*, typically  
22  
23 216 showed no bias in sex ratios with the exception of a male bias in the overwintering 2007 generation  
24  
25  
26  
27 217 and a female bias in the summer 2010 generation.

## 28 29 218 **Discussion**

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31  
32 219 A total of 27 species in six chalcid families (Eurytomidae, Pteromalidae, Torymidae,  
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34 220 Eupelmidae, Ormyridae, Eulophidae) were found to be associated with *D. kuriphilus* galls during  
35  
36 221 the five year period 2006-2010. Seventeen of these species were not recorded by Aebi *et al.* (2006)  
37  
38 222 so represent recent additions to the parasitoid community attacking this pest in Italy, although four  
39  
40 223 of them are cryptic species revealed by molecular analyses so may have been present but simply  
41  
42 224 unrecognised in earlier surveys (for example see Aebi *et al.*, 2007). Aebi *et al.* (2006) recorded five  
43  
44 225 further species associated with *D. kuriphilus* during the early years of the pest's establishment that  
45  
46 226 were not recorded in this study (*Torymus scutellaris* (Walker), *T. auratus* (Müller), *Sycophila*  
47  
48 227 *iracemae* Nieves-Aldrey, *Mesopolobus mediterraneus* (Mayr) and *Baryscapus pallidae* Graham;  
49  
50  
51 228 Table 2), bringing the total number of parasitoid species known to attack *D. kuriphilus* in Italy to  
52  
53 229 32. Many of these species appear to parasitise *D. kuriphilus* only occasionally and therefore may be  
54  
55 230 at a very early stage in their recruitment onto this novel host. However, four species (*M. dorsalis*, *E.*  
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57 231 *urozonus*, *E. annulatus* and *E. pistaciae*) are more abundant and appear to have incorporated *D.*  
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59 232 *kuriphilus* into their regular host range.

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3 233 In its native distribution *D. kuriphilus* populations are kept at low densities by natural  
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6 234 enemies; in contrast in regions where it has invaded (Japan, South Korea and the USA) the attack  
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8 235 rates of indigenous parasitoid species have remained low many years after the arrival of the pest  
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10 236 (typically less than 2%) (Murakami *et al.*, 1995; Ito & Hijii, 2000; Stone *et al.*, 2002; Aebi *et al.*,  
11  
12 237 2007). This study confirms the same pattern in Italy more than 10 years after *D. kuriphilus* first  
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15 238 invaded, despite the species richness of the associated parasitoid community. The emergence rate  
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17 239 across all indigenous parasitoids from the summer galls was typically 2-3 individuals per 100 galls,  
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19  
20 240 and although the emergence rate from winter galls increased over the study period it still remained  
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22 241 relatively low (6 individuals per 100 galls). In addition, since *D. kuriphilus* galls are multilocular,  
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25 242 any individual female parasitoid may lay multiple eggs within a single gall so the overall rate of  
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27 243 parasitism may well be even lower than our emergence data suggest. As a result, it appears unlikely  
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29 244 that current activities of indigenous parasitoids will be able to bring about control of this serious  
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31  
32 245 pest. Given the economic and ecological damage caused by *D. kuriphilus* and considering the lack  
33  
34 246 of alternative effective control strategies (EFSA, 2010), this ineffective control by indigenous  
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36 247 natural enemies highlights the need for biological control using the exotic parasitoid *T. sinensis*  
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38  
39 248 (Quacchia *et al.*, 2008; Gibbs *et al.*, 2011).

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41 249 The degree to which native parasitoids may help impose some control over *D. kuriphilus* also  
42  
43 250 depends on how well integrated this pest becomes into the oak gall community. The data presented  
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45  
46 251 here indicate that although some recruitment of oak gall parasitoids has occurred, there is still a  
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48 252 mismatch between the phenology of gall development by the univoltine *D. kuriphilus* and the  
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50  
51 253 emergence times of native natural enemies. This pattern is also found for parasitoids that are shared  
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53 254 with oak galls in the pest's native China (Murakami *et al.*, 1980). The presence of this phenological  
54  
55 255 mismatch implies that parasitoid exchange between chestnut galls and oak galls is an ongoing  
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57  
58 256 process, with occasional use of chestnut galls by a community that has evolved around the use of  
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60 257 bivoltine oak galls. However, the extremely high abundance of *D. kuriphilus* galls in its invaded  
258 European range represents a massive unexploited resource available for any lineages within

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3 259 parasitoid species that have a phenology more suited to that of *D. kuriphilus*. This could provide  
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6 260 these lineages with a selective advantage, potentially leading to the development of genetically  
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8 261 discrete host-associated ecotypes, one attacking oak galls and the other cycling on chestnut galls.  
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10 262 Such a scenario implies that over time the communities centred around the two resources of oak  
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12 263 galls and chestnut galls remain relatively distinct, with little exchange of individuals between them.  
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15 264 However, genetic data are required to establish whether this may be a possibility or whether  
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17 265 parasitoids consider oak- and chestnut-galling cynipids to be ecologically equivalent hosts within a  
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20 266 single community.

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22 267 Our data provide some preliminary suggestions that *D. kuriphilus* has been integrated into the  
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24 268 oak gall community to a sufficient extent that it has impacted upon the behaviour of parasitoids.  
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27 269 The observed biases in sex ratios for some parasitoid species suggest that female parasitoids may be  
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29 270 altering their laying behaviour in response to the presence of this novel host. However, this remains  
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31  
32 271 untested since we did not assess the sex ratios of the corresponding species emerging from native  
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34 272 oak galls, so the observed biases may actually reflect a population-level bias apparent across all  
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36 273 hosts. Nevertheless, given its novelty, native parasitoids may view *D. kuriphilus* as a resource of  
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39 274 unpredictable or lower quality, and therefore individuals may alter their laying behaviour to take  
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41 275 advantage of this novel yet abundant host whilst minimising the risk to overall fitness (Charnov *et*  
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43 276 *al.*, 1981). In this case the male-biased sex ratio we observed emerging from overwintering galls  
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46 277 may be due to the high relative abundance of chestnut galls in infested areas that act as a sink for  
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48 278 excess male eggs that otherwise would not be laid, a phenomenon associated with other invading  
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51 279 gallwasp species at high abundance (Hails & Crawley, 1991; Schönrogge *et al.*, 2000).

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53 280 Such integration of the invading *D. kuriphilus* into the native oak gall community has broader  
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55 281 implications for the evolution of this community. All the parasitoids attacking *D. kuriphilus* have  
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58 282 very broad host ranges, a general pattern also seen during the recruitment of parasitoids onto other  
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60 283 invading gallwasps (Stone *et al.*, 1995). Our data confirm the presence of some generalist parasitoid  
284 species that were predicted to recruit onto chestnut galls by Aebi *et al.* in 2006, and we could

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3 285 reasonably expect further generalist species to start attacking *D. kuriphilus* in the near future. In  
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6 286 addition, although there is limited evidence for the recruitment of cynipid inquilines onto *D.*  
7  
8 287 *kuriphilus* galls (Aebi *et al.*, 2006), if these important constituents of the oak gall community were  
9  
10 288 to start utilising chestnut galls we could also expect them to bring along greater parasitoid diversity  
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12 289 (Schönrogge *et al.*, 1996) and hence tighten further the trophic links between oak and chestnut gall  
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15 290 communities. Given the very large population sizes of *D. kuriphilus* that can act as a significant  
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17 291 breeding ground for parasitoids, the presence of these trophic links means there is the potential for  
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20 292 severe negative impacts on native oak gall cynipids through the process of apparent competition  
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22 293 mediated through shared parasitoid species (Holt, 1977). The larger population sizes that may result  
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24 294 from increased use of the abundant *D. kuriphilus* could in turn lead to increased levels of parasitism  
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27 295 imposed upon native oak gallers, potentially driving their populations locally extinct (Hassel, 2000)  
28  
29 296 or inducing severe perturbations in the functioning of native communities (Henneman & Memmott,  
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31 297 2001). Such effects may be particularly likely to occur in the oak-chestnut galler community, given  
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34 298 that the parasitoid species most frequently attacking *D. kuriphilus* have broad host ranges within  
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36 299 native communities (see for example Askew, 1966). In addition, at least one of the commonly  
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39 300 encountered species, *E. urozonus*, is known also to attack leaf miners (Askew & Nieves-Aldrey,  
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41 301 2000), so impacts of increased parasitoid attack could extend into the wider community of insects  
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43 302 on both chestnuts and oaks.

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46 303 One further complication is that one of the commonest parasitoids attacking *D. kuriphilus* is  
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48 304 *E. urozonus*, a species that can act as a hyperparasitoid and therefore can impose mortality upon  
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51 305 multiple trophic levels within a community. A similar phenomenon has recently been observed for  
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53 306 the parasitoid *Ormyrus labotus* Walker in the USA (Cooper & Rieske, 2011); in addition to  
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55 307 parasitising *D. kuriphilus*, this species also attacks the introduced biological control agent *T.*  
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57  
58 308 *sinensis*. Hence it is imperative that monitoring of the community associated with *D. kuriphilus*  
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60 309 continues and that action is taken to minimise the impact this invader has on the wider ecosystem.

310 Furthermore, the potential for apparent competition can be examined in more detail using genetic

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3 311 data to assess levels of gene flow among parasitoid populations attacking native oak galls and those  
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6 312 attacking chestnut galls. This would allow rates of parasitoid exchange between the different hosts  
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8 313 to be assessed, and therefore the degree to which parasitoids from chestnut galls could impact upon  
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10 314 native communities.

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14  
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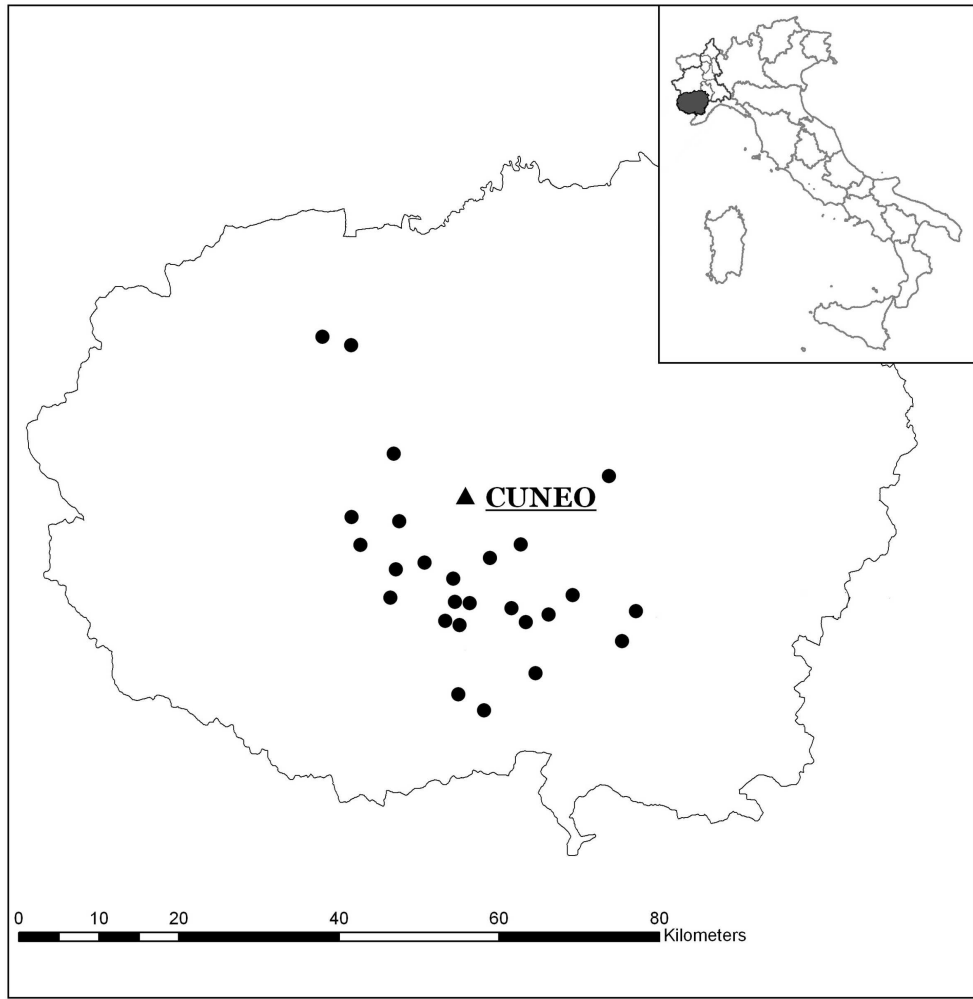
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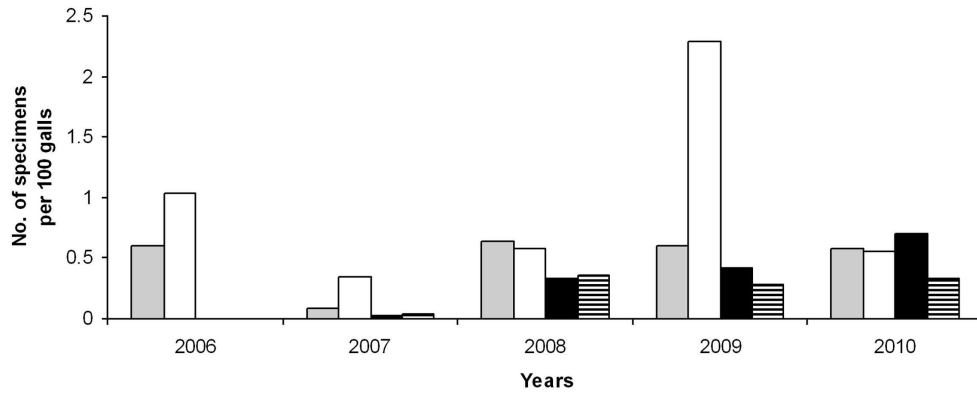
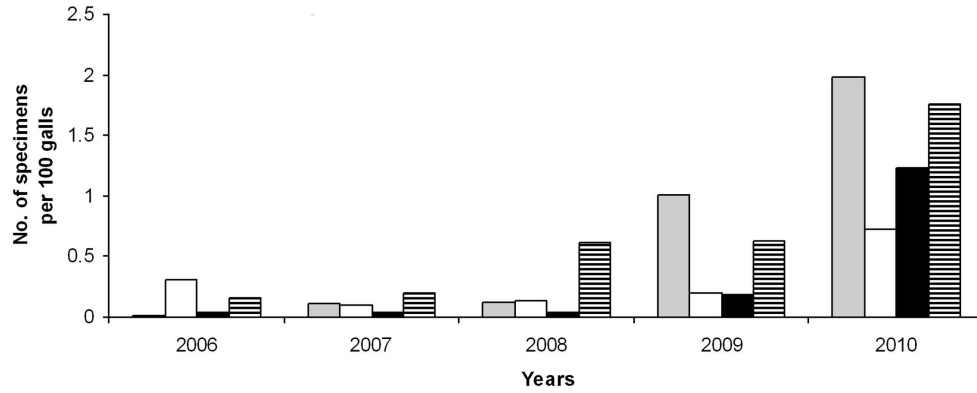
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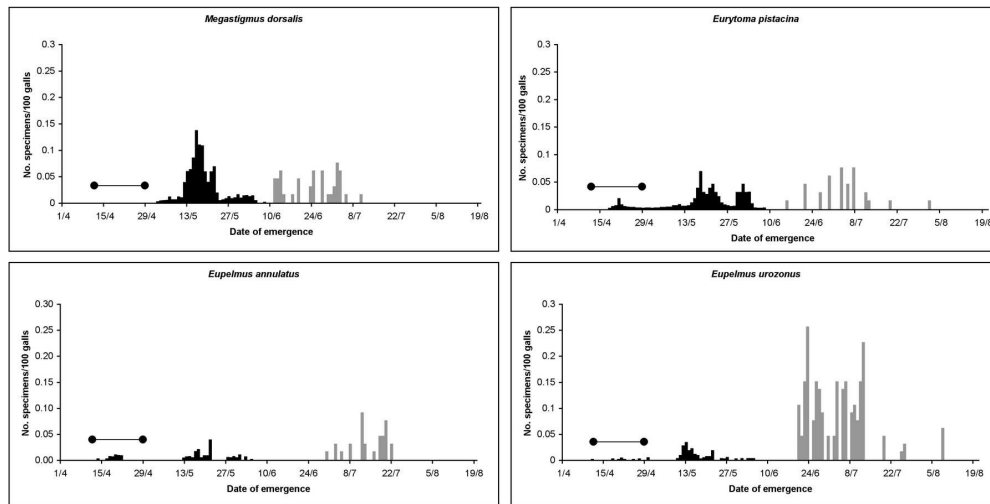
Location of the 26 sampling sites in Cuneo province, with inset showing the location of Cuneo province within Italy.  
204x209mm (300 x 300 DPI)



Emergence rates of the four most common parasitoid species attacking *Dryocosmus kuriphilus* galls in Cuneo province, Italy, over the years 2006-2010. The upper graph shows winter emergence, the lower one shows summer emergence. Shading of bars indicates species: grey *Megastigmus dorsalis*, white *Eupelmus urozonus*, black *Eupelmus annulatus*, stripes *Eurytoma pistaciae*.  
196x183mm (300 x 300 DPI)



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Seasonal patterns of emergence of the four most common parasitoid species attacking *Dryocosmus kuriphilus* galls in Cuneo province, Italy, in 2009. Black bars show emergence from withered galls collected in winter 2008-2009, grey bars show emergence from newly formed galls collected in summer 2009; the line indicates the growth period of *D. kuriphilus* galls.  
152x78mm (300 x 300 DPI)

View Only





Table 2. Parasitoid species attacking the chestnut gallwasp *Dryocosmus kuriphilus* in north-western Italy. Species names in bold indicate cryptic species pairs which molecular data resolve; not all individuals collected each year from these species pairs were sequenced, so the presence of the first mentioned species indicates presence of the corresponding morpho-species. Data for the years 2002-2005 are from Aebi *et al.*, 2006.

| Species                                  | Family       | 2002-2005 | 2006 | 2007 | 2008 | 2009 | 2010 |
|--|--------------|-----------|------|------|------|------|------|
| <i>Aprostocetus</i> sp.                  | Eulophidae   |           | X    | X    | X    | X    | X    |
| <i>Aulogymnus arsames</i>                | Eulophidae   |           |      |      |      | X    |      |
| <i>Aulogymnus</i> sp.                    | Eulophidae   |           |      | X    | X    | X    | X    |
| <i>Baryscapus pallidae</i>               | Eulophidae   | X         |      |      |      |      |      |
| <i>Baryscapus</i> sp.                    | Eulophidae   |           |      |      |      |      | X    |
| <i>Pediobius chilaspidis</i>             | Eulophidae   |           |      | X    |      |      |      |
| <i>Pediobius saulius</i>                 | Eulophidae   |           |      |      | X    |      | X    |
| <i>Pediobius</i> sp.                     | Eulophidae   |           |      | X    | X    |      | X    |
| <b><i>Eupelmus annulatus</i>*</b>        | Eupelmidae   |           | X    | X    | X    | X    | X    |
| <b><i>Eupelmus spongipartus</i>*</b>     | Eupelmidae   |           |      |      |      | X    |      |
| <i>Eupelmus splendens</i>                | Eupelmidae   |           |      | X    |      | X    |      |
| <b><i>Eupelmus urozonus</i></b>          | Eupelmidae   | X         | X    | X    | X    | X    | X    |
| <b><i>Eupelmus fulvipes</i></b>          | Eupelmidae   |           |      |      |      | X    |      |
| <b><i>Eurytoma brunniventris</i></b>     | Eurytomidae  | X         |      | X    | X    | X    | X    |
| <b><i>Eurytoma adleriae</i></b>          | Eurytomidae  |           |      |      |      |      | X    |
| <i>Eurytoma pistaciae</i>                | Eurytomidae  | X         | X    | X    | X    | X    | X    |
| <i>Sycophila variegata</i>               | Eurytomidae  | X         | X    | X    | X    | X    | X    |
| <i>Sycophila biguttata</i>               | Eurytomidae  | X         |      | X    |      | X    | X    |
| <i>Sycophila iracemae</i>                | Eurytomidae  | X         |      |      |      |      |      |
| <i>Ormyrus nitidulus</i>                 | Ormyridae    |           |      |      |      | X    |      |
| <i>Ormyrus pomaceus</i>                  | Ormyridae    | X         |      |      |      | X    | X    |
| <i>Cecidostiba</i> sp.                   | Pteromalidae |           |      |      | X    |      | X    |
| <i>Mesopolobus amaenus</i>               | Pteromalidae |           |      |      | X    |      |      |
| <i>Mesopolobus mediterraneus</i>         | Pteromalidae | X         |      |      |      |      |      |
| <i>Mesopolobus sericeus</i>              | Pteromalidae | X         |      | X    | X    | X    | X    |
| <i>Mesopolobus tarsatus</i>              | Pteromalidae | X         |      | X    |      | X    |      |
| <i>Mesopolobus tibialis</i>              | Pteromalidae |           |      | X    |      |      |      |
| <b><i>Megastigmus dorsalis</i> (sp1)</b> | Torymidae    | X         | X    | X    | X    | X    | X    |
| <b><i>Megastigmus dorsalis</i> (sp2)</b> | Torymidae    |           |      |      |      | X    |      |
| <i>Torymus auratus</i>                   | Torymidae    | X         |      |      |      |      |      |
| <i>Torymus flavipes</i>                  | Torymidae    | X         |      | X    |      |      |      |
| <i>Torymus scutellaris</i>               | Torymidae    | X         |      |      |      |      |      |

\*Bouček's (1970) consideration of *Eupelmus annulatus* and *E. spongipartus* as synonyms appears to be incorrect and the names do represent two distinct species (Gibson, 2011).

Table 3. Number of females and males of the four most abundant parasitoid species emerging from *Dryocosmus kuriphilus* galls in north-western Italy in the period 2006-2010. The observed sex ratios were tested against an expected 50:50 ratio (all d.f. = 1, \*P<0.05, \*\*P<0.01, \*\*\*P<0.001; NS=not significant).

| 2006                        | winter |      |           | summer |    |          |
|-----------------------------|--------|------|-----------|--------|----|----------|
|                             | F      | M    | $\chi^2$  | F      | M  | $\chi^2$ |
| <i>Megastigmus dorsalis</i> | 0      | 1    | NS        | 22     | 2  | 16.67*** |
| <i>Eupelmus urozonus</i>    | 12     | 16   | NS        | 38     | 3  | 29.88*** |
| <i>Eupelmus annulatus</i>   | 3      | 0    | NS        | -      | -  | -        |
| <i>Eurytoma pistaciae</i>   | 6      | 8    | NS        | -      | -  | -        |
| 2007                        | winter |      |           | summer |    |          |
|                             | F      | M    | $\chi^2$  | F      | M  | $\chi^2$ |
| <i>Megastigmus dorsalis</i> | 14     | 60   | 28.59***  | 8      | 12 | NS       |
| <i>Eupelmus urozonus</i>    | 20     | 45   | 9.62**    | 46     | 38 | NS       |
| <i>Eupelmus annulatus</i>   | 18     | 3    | 10.71**   | 4      | 2  | NS       |
| <i>Eurytoma pistaciae</i>   | 32     | 93   | 29.77***  | 2      | 8  | NS       |
| 2008                        | winter |      |           | summer |    |          |
|                             | F      | M    | $\chi^2$  | F      | M  | $\chi^2$ |
| <i>Megastigmus dorsalis</i> | 11     | 86   | 57.99***  | 20     | 9  | 4.17*    |
| <i>Eupelmus urozonus</i>    | 29     | 82   | 25.31***  | 15     | 11 | NS       |
| <i>Eupelmus annulatus</i>   | 10     | 19   | NS        | 9      | 6  | NS       |
| <i>Eurytoma pistaciae</i>   | 241    | 245  | NS        | 11     | 5  | NS       |
| 2009                        | winter |      |           | summer |    |          |
|                             | F      | M    | $\chi^2$  | F      | M  | $\chi^2$ |
| <i>Megastigmus dorsalis</i> | 227    | 1115 | 587.59*** | 28     | 12 | 6.40*    |
| <i>Eupelmus urozonus</i>    | 78     | 177  | 38.44***  | 96     | 57 | 9.94**   |
| <i>Eupelmus annulatus</i>   | 77     | 165  | 32.00***  | 25     | 3  | 17.29*** |
| <i>Eurytoma pistaciae</i>   | 391    | 446  | NS        | 13     | 6  | NS       |
| 2010                        | winter |      |           | summer |    |          |
|                             | F      | M    | $\chi^2$  | F      | M  | $\chi^2$ |
| <i>Megastigmus dorsalis</i> | 401    | 1300 | 475.13*** | 15     | 9  | NS       |
| <i>Eupelmus urozonus</i>    | 446    | 180  | 113.03*** | 17     | 6  | 5.26*    |
| <i>Eupelmus annulatus</i>   | 400    | 652  | 60.37***  | 21     | 8  | 5.83*    |
| <i>Eurytoma pistaciae</i>   | 757    | 754  | NS        | 12     | 2  | 7.14**   |

Table S1. Emergence data for the 10 parasitoid species found to attack *Dryocosmus kuriphilus* galls regularly in north-western Italy during the period 2006-2010. Both the total number of specimens (ns) and the standardised emergence rate (er; number of adults emerging per 100 galls) are presented.

|                               | <u>2006</u> |      | <u>2007</u> |      | <u>2008</u> |      | <u>2009</u> |      | <u>2010</u> |      |        |      |      |      |     |      |      |      |     |      |
|-------------------------------|-------------|------|-------------|------|-------------|------|-------------|------|-------------|------|--------|------|------|------|-----|------|------|------|-----|------|
|                               | winter      |      | summer      |      | winter      |      | summer      |      | winter      |      | summer |      |      |      |     |      |      |      |     |      |
|                               | ns          | er   | ns          | er   | ns          | er   | ns          | er   | ns          | er   | ns     | er   |      |      |     |      |      |      |     |      |
| <i>Megastigmus dorsalis</i>   | 1           | 0.01 | 24          | 0.61 | 74          | 0.11 | 20          | 0.08 | 97          | 0.12 | 29     | 0.64 | 1342 | 1.01 | 40  | 0.60 | 1701 | 1.98 | 24  | 0.58 |
| <i>Eurytoma pistaciae</i>     | 14          | 0.16 | -           | -    | 125         | 0.19 | 10          | 0.04 | 486         | 0.61 | 16     | 0.36 | 837  | 0.63 | 19  | 0.28 | 1511 | 1.76 | 14  | 0.34 |
| <i>Eupelmus annulatus</i>     | 3           | 0.03 | -           | -    | 21          | 0.03 | 6           | 0.02 | 29          | 0.04 | 15     | 0.33 | 242  | 0.18 | 28  | 0.42 | 1052 | 1.23 | 29  | 0.70 |
| <i>Eupelmus urozonus</i>      | 28          | 0.31 | 41          | 1.04 | 65          | 0.10 | 84          | 0.35 | 111         | 0.14 | 26     | 0.58 | 255  | 0.19 | 153 | 2.29 | 626  | 0.73 | 23  | 0.55 |
| <i>Sycophila variegata</i>    | -           | -    | 6           | 0.15 | 1           | 0.00 | -           | -    | 4           | 0.01 | 3      | 0.07 | 18   | 0.01 | 2   | 0.03 | 74   | 0.09 | 5   | 0.12 |
| <i>Sycophila biguttata</i>    | -           | -    | 3           | 0.08 | -           | -    | 6           | 0.02 | -           | -    | 2      | 0.04 | 3    | 0.00 | 1   | 0.01 | 33   | 0.04 | -   | -    |
| <i>Eurytoma brunniventris</i> | -           | -    | -           | -    | -           | -    | 50          | 0.21 | 1           | 0.00 | 9      | 0.20 | 10   | 0.01 | -   | -    | 1    | 0.00 | -   | -    |
| <i>Mesopolobus sericeus</i>   | -           | -    | -           | -    | 2           | 0.00 | -           | -    | 19          | 0.02 | -      | -    | 10   | 0.01 | -   | -    | 161  | 0.19 | 15  | 0.36 |
| <i>Aulogymnus</i> sp.         | -           | -    | -           | -    | 31          | 0.05 | -           | -    | 21          | 0.03 | -      | -    | 26   | 0.02 | -   | -    | 16   | 0.02 | -   | -    |
| <i>Aprostocetus</i> sp.       | -           | -    | 23          | 0.58 | 47          | 0.07 | -           | -    | 1           | 0.00 | -      | -    | 5    | 0.00 | -   | -    | 16   | 0.02 | -   | -    |
| <i>total</i>                  | 92          | 0.51 | 97          | 2.45 | 366         | 0.56 | 176         | 0.73 | 769         | 0.97 | 100    | 2.22 | 2748 | 2.08 | 243 | 3.64 | 5191 | 6.05 | 110 | 2.65 |