Biological control of the chestnut gall wasp with *T. sinensis*: A mathematical model

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ABSTRACT

The Asian chestnut gall wasp *Dryocosmus kuriphilus*, native of China, has become a pest when it appeared in Japan, Korea, and the United States. In Europe it was first found in Italy, in 2002. In 1982 the host-specific parasitoid *Torymus sinensis* was introduced in Japan, in an attempt to achieve a biological control of the pest. After an apparent initial success, the two species seem to have locked in predator–prey cycles of decadal length. We have developed a spatially explicit mathematical model that describes the seasonal time evolution of the adult insect populations, and the competition for finding egg deposition sites. In a spatially homogeneous situation the model reduces to an iterated map for the egg density of the two species. While, for realistic parameters, the map would support the hypothesis of biological control, the full model, in the same parameter range, does not give such a clear-cut answer. In particular, according to the spatially explicit model, the introduction of *T. sinensis* would spark a traveling wave of the parasitoid population that destroys the pest on its passage. Then, depending on the value of the diffusion coefficients of the two species, the pest may later be able to re-colonize the empty area left behind the wave. When this occurs the two populations do not seem to attain a state of spatial homogeneity, but produce an ever-changing pattern of traveling waves.

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1. Introduction

Since its first report in 2002 the Asian chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) is affecting many chestnut ecosystems in Europe and its range is continuously expanding. Native of China, it established as a pest in the mid 20th century in several countries, being reported in Japan (1941) (Moriya et al., 2003), in Korea (1958) (Cho and Lee, 1963), in the United States (1974) (Rieske, 2007), in Nepal (1999) (Abe et al., 2007), and in Canada (2012) (Huber and Read, 2012).

In Europe, *D. kuriphilus* was first found in Italy and reported only in 2002 (Brussino et al., 2002). It was added to the European Plant Protection Organization (EPPO) A2 Action list (EPPO, 2005) in 2003. Despite the European Commission Decision 2006/464/EC of 27 June
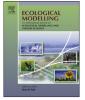
2006 to put into place provisional emergency measures to prevent the introduction into and the spread within the community of *D. kuriphilus*, the pest is now widely distributed in Italy and has become established in many other European countries including Austria (2013), Croatia (2010), Czech Republic and Slovakia (2012), France (2005), Germany (2013), Hungary (2013), Portugal (2014), Slovenia (2005), Spain (2012), Switzerland (2009), Turkey (2014), the United Kingdom (2015) and Belgium (2016) (EFSA, 2010; EPPO, 2013, 2015a, 2016). In the Netherlands it was accidentally imported through nursery trees (2010) and then promptly detected and eradicated by destroying the few affected plants (NPPO, 2013), but recently a new outbreak has been detected close to the German border (EPPO, 2015b). Since *D. kuriphilus* has shown its ability to spread rapidly and is successfully established in several countries, further establishment is likely in Europe anywhere there is availability of the host plants *Castanea* spp. (EFSA, 2010).

The chestnut gall wasp is a univoltine and thelytokous species (Moriya et al., 1989), and lays eggs in buds during summer. The hatched larvae induce the formation of greenish-red galls, which develop at the time of budburst in the following early spring on new shoots (Ôtake, 1980), suppressing shoot elongation and

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causing twig dieback. Severe reduction of fruiting with yield losses due to insect attacks have been estimated to reach between 65% and 85% in northern Italy (Bosio et al., 2013; Battisti et al., 2014). However, no evidence was found to confirm tree mortality. A gradual reduction in vigor in the longer term is the likely consequence of annual infestation by the gall wasp, causing a gradual reduction in biomass (EFSA, 2010).

Early attempts of biological control of the pest were performed in Japan (Murakami et al., 1977; Murakami, 1981) and in the USA (Rieske, 2007) by the introduction of *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), a chinese parasitoid described by Kamijo (1982). In its native environment it is only one among many species of natural parasitoids of *D. kuriphilus* (Murakami et al., 1980), but it appears to be very well synchronized with the life cycle of the pest, making it a strong candidate as a biological control agent (Murakami, 1981). In addition, outside China, it was believed to be host-specific, although its host range was never studied or tested in detail (Murakami et al., 1977; Gibbs et al., 2011). Recently, a large-scale survey in northern Italy found a few specimens of *T. sinensis* emerging from oak galls of the non-target host *Biorhiza pallida* Olivier. All evidence, however, still suggests that *D. kuriphilus* is by far the preferred host, and parasitism of other species occurs only exceptionally, possibly as a response to scarcity of its primary host (Ferracini et al., 2015a).

T. sinensis reproduces sexually, and by arrhenotokous parthenogenesis if there is lack of mating. It is reported as univoltine, like its host. However, recent preliminary investigations highlighted that a very small fraction of the insect population may undergo a prolonged diapause extended for 12 months, mainly as late instar larva (Ferracini et al., 2015b). After emergence, which takes place in early spring, and mating, the female lays eggs inside the larval chamber of newly formed galls, one egg per host larva. Although in controlled conditions occasional multiple eggs per host larva have been reported by an early study (Piao and Moriya, 1992), we have never found more than one egg per host larva while dissecting galls collected in the field. After hatching, the larva feeds ectoparasitically on the host larva, and it pupates in the host larval chamber during winter.

T. sinensis was introduced in Japan from China (Murakami et al., 1977, 1980; Moriya et al., 2003). After its release, it dispersed successfully alongside expanding *D. kuriphilus* populations. In Japan *D. kuriphilus* may also be subject to varying levels of parasitism from native insects, most notably *Torymus beneficus* Yasumatsu & Kamijo and several species of the genus *Eupelmus* (Murakami and Gyoutoku, 1995; Moriya et al., 2003) that, however, are unable to control the pest. Monitoring of test orchards showed that after about 6–18 years from the introduction of *T. sinensis*, the pest population declined to levels as low as to be practically undetectable, giving rise to claims of success in biologically controlling the infestation (Moriya et al., 1989, 2003; Murakami et al., 2001). However, continuous monitoring of the first release site over 25 years shows three successive peaks in the population of *D. kuriphilus*, shortly followed by peaks in the population of *T. sinensis* (Moriya, personal communication). In the USA, several Asian *Torymus* species were released in 1977 in southeastern Georgia, but the release was not followed by any monitoring. The first accounts of the successful establishment of *T. sinensis* in the United States were published only thirty years later (Cooper and Rieske, 2007; Rieske, 2007). In spite of the abundant presence of *T. sinensis*, and of *Ormyrus labotus* Walker (a native insect that was shown to easily parasitize *D. kuriphilus* galls), the pest could be found in most of the southern Appalachian range, with satellite infestations in Ohio and Pennsylvania.

The European chestnut (*Castanea sativa* Mill.) is one of the most important broad-leaved species in Italy: chestnut stands amount to 788,400 ha, which represents 9% of the Italian forests (Graziosi and Santi, 2008). Due to the report of the gall wasp

in 2002 and in consideration of the long-established economic importance of chestnut throughout the country for fruit and wood production, a collaboration was started with Japanese researchers and a biological control program was initiated in 2005 with the release in infested orchards of Japan-imported *T. sinensis* specimens (Quacchia et al., 2008). Following the Japanese and Italian experiences, reporting the establishment of a sizable population of *T. sinensis* vigorously parasitizing the galls of *D. kuriphilus*, recent releasing programs were performed in Croatia, France and Hungary (Borowiec et al., 2014; Matošević et al., 2014), as well as test releases in Spain and Portugal (Juan Ramón Boyero at Junta de Andalucia, personal communication, Associação Portuguesa da Castanha, 2015).

Although in Europe there exist several native species of Hymenoptera capable of parasitizing *D. kuriphilus* galls, all of them have a very large host range, and suffer by a mismatch between their emergence times and the development of the galls. They are therefore unable to act effectively as biological control agents (Aebi et al., 2006, 2007; Quacchia et al., 2013; Alma et al., 2014).

In the present paper we develop a mathematical model of the interaction between *T. sinensis* and *D. kuriphilus* aiming at developing a tool for understanding and evaluating the effectiveness of biological control programs based on the release of *T. sinensis* in woods and orchards infested by *D. kuriphilus*.

In particular we would like to investigate whether *T. sinensis* should be expected to be able, alone, to maintain its population to levels at least as low as to produce no harm, or if such expectations are over optimistic. The fact that *T. sinensis* is extremely well synchronized with *D. kuriphilus*, that outside China it acts almost perfectly as host-specific, and that in Europe its abundance appears to be limited only by the availability of its host, with a very low mortality during all its life stages, allows hopes for a rapid, complete, and permanent control of the pest. However, the experiences of both Japan and the USA warn that the effectiveness of *T. sinensis* might be less perfect than one would wish it to be. In the case of Japan the imperfect control of *D. kuriphilus* has been ascribed to a high mortality of *T. sinensis* by hyperparasitism (Murakami and Gyoutoku, 1991). In Europe hyperparasitism is only occasional (Quacchia et al., 2013), which leaves more room for hopes of obtaining a control.

In order to have a flexible tool, our model, in its full form, is hybrid discrete–continuous in time and spatially explicit. In an abstract setting, a class of models of this sort for a single species has been discussed by Lewis and Li (2012). Our model describes the host–parasitoid interplay of two species (namely *T. sinensis* and *D. kuriphilus*). For both species the time-continuous part of the model describes the seasonal dispersal of the adult insect population, and the inter-specific competition for finding egg deposition sites. The time-discrete (or "impulsive") part describes the overwintering of the larvae. In a spatially-homogeneous situation the model may be rigorously reduced to an iterated map quantifying the egg density of the two species, whose properties are studied with a combination of analytic and numerical techniques. The full, spatially-explicit model is studied by means of numerical simulations in one and two spatial dimensions. The comparison between the dynamics of the iterated maps and of the full model suggests a diffusion-based mechanisms that may give rise, under certain conditions, to repeated waves of full infestation followed by near disappearance of the pest and of its parasitoid, on time scales that depend not only on the physiological and ecological parameters, but also on the size and geometry of the wood.

The rest of the paper is organized as follows: the mathematical model is developed in Section 2; the results obtained from the model are reported in detail in Section 3; finally they are summarized in Section 4, together with some speculative considerations.