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Effects of an asynchronous alien host on a native host-parasitoid system

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ABSTRACT

We present a discrete-generation model to study the effect of a seasonally asynchronous alien host on the population dynamics of a native host/parasitoid system. We assume that i) the native host and parasitoid are seasonally synchronous; ii) there is no direct competition for resources between the two host species (one native, one alien); and iii) the introduced alien host population (the alternative host) is in an invasive stage and, consequently, it is not subject to any density-dependent regulation. In our model, variations in the annual number of generations (voltinism) of the alien host greatly alter the dynamics of the native host/parasitoid interaction. When the alien host is synchronous with the native host, the parasitoid is favoured, and the native host population decreases until reaching a new, lower equilibrium or becoming extinct. By contrast, when alien and native hosts are asynchronous with each other, there are population oscillations of the native community members compatible with the pulsating availability of the alien host and, under specific conditions, the parasitoid may rapidly become extinct.

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1. Introduction

The chestnut gall wasp, *Dryocosmus kuriphilus*, is a peculiar cynipid. Unlike the majority of species in the tribe Cynipini, it does not form galls on oaks (*Quercus*) but on chestnuts (*Castanea*). Moreover, *D. kuriphilus* has lost the typical feature of its tribe, heterogony (the alternation between sexually and asexually reproducing generations) and has become parthenogenetic (Stone et al., 2002). As such, while oak cynipids are commonly bivoltine (i.e. they complete a sexual-asexual cycle in a single year) (Askew, 1984), the chestnut gall wasp is univoltine (Moriya et al., 2003).

Although *D. kuriphilus* does not seem to have any serious impact on chestnut trees in its native China (Murakami, 1980), it has become a major pest of chestnut trees in the areas where it was accidentally introduced. Heavy attack can reduce fruit yield by more than a half (Payne et al., 1983), as well as affect tree vigour and wood production (Kato and Hijjii, 1997). The chestnut gall wasp has invaded Japan (since 1941) and Korea (1958)

(Yasumatsu, 1951; Shiraga, 1951; Cho and Lee, 1963), North America (1974) (Payne et al., 1975; Cooper and Rieseke, 2007), and more recently Europe starting from Italy (2002) (Brussino et al., 2002).

In areas of its introduction, the chestnut gall wasp rapidly recruited many parasitoid species, mostly from those attacking native oak gall wasps (Aebi et al., 2006; Cooper and Rieseke, 2007; Kos et al., 2015), but dramatic fluctuations in native parasitoid attack rates and community composition have frequently been reported (Ôtake, 1989; Quacchia et al., 2013; Francati et al., 2015; Colombari and Battisti, 2016). In fact, native parasitoids generally have failed to reduce the populations of *D. kuriphilus* (Ôtake et al., 1984; Stone et al., 2002). Successful reduction of the pest populations was obtained only after the introduction of the Chinese Torymid, *Torymus sinensis*, a species which has both high host specificity and a life cycle closely adapted to its host (Moriya et al., 2003; Cooper and Rieseke, 2007; Ferracini and Alma, 2015; Matošević et al., 2017).

The life-cycles of the native parasitoids are only partially synchronized with that of the chestnut gall wasp. In particular, many native parasitoid species are at least bivoltine and, hence, their first larval generation can attack both the single generation of *D. kuriphilus* and the first generation (sexual) of the native Cynipids on oak, whereas their second larval generation can attack only the second generation (asexual) of the native hosts. Consequently, the

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second generation of the last ones is exposed to a particularly large number of adult parasitoids, i.e. those that emerged from both the chestnut gall wasp, as well as the first generation (sexual) of native hosts.

We suspect that the above seasonal asynchrony could play a crucial role in the interactions between the invader and the local community, and could include both direct effects on parasitoids and indirect effects on the native hosts that share the same parasitoids. This question surely has general interest, as demonstrated in the two following cases.

The armoured scales of hemlock, *Fiorina externa* and *Nuculaspis tsugae*, are two alien pests, invasive in USA from Japan, that occur on the same host tree (*Tsuga*, hemlock) and also share an introduced parasitoid, *Aspidiotiphagus citrinus*. In the native homeland the two species of scales and the parasitoid have two synchronized generations per year (all are bivoltine) and the peak emergence of adult parasitoids coincides with the peak abundance of susceptible instars of both hosts. However, in the climate of northeastern USA one of the hosts, *F. externa* (the most abundant of the host species), has only one generation per year; it coincides with the first generation of both the parasitoid and with the other scale. Thus, the adult parasitoids emerging from summer generations find only *N. tsugae* as a suitable host. Consequently, *N. tsugae* is dramatically excluded from the system as extensively demonstrated by McClure (McClure, 1981, 1988).

A more complex case study involves the recent invasion in W-Europe of the horse chestnut leaf-miner, *Cameraria ohridella* (Gilbert et al., 2005; Valade et al., 2009) that shares many species of parasitoids with native leaf miners (Girardoz et al., 2006). The populations of the invasive moth are so high that an unusually large number of parasitoids are produced at each generation. However, there is a considerable time lag between the emergence of the native parasitoids in spring and the appearance of suitable instars of the invasive alien leaf-miner in early summer (Grabenweger, 2004). Consequently, early-occurring native leaf-miners, that in spring represent the sole available resource, are exposed to a particularly large number of the shared parasitoids. In this context, Péré et al. (2009) support the opinion that the spring generation of parasitoids has the potential to significantly affect populations of early-occurring native leaf-miners. Indeed a lower abundance and a lower species richness of local leaf-miner communities was registered in the vicinity of horse-chestnut trees attacked by *C. ohridella*.

In all these cases there are not only differences between the timing of the susceptible stages of the host on the one hand and the foraging adult parasitoids on the other (Forrest and Miller-Rushing, 2010; Miller-Rushing et al., 2010; Johansson et al., 2015), but also between the number of generations per year, namely differences in voltinism (Bradshaw, 1974; Douth et al., 1976; Tauber et al., 1986). While the influence of phenological asynchronies on the host/parasitoid systems has been investigated by means of theoretical models (Münster-Swendsen and Nachman, 1978; Godfray et al., 1994), differences in the number of generations per year (voltinism) have not been included in these studies and are in general scarcely explored. In this context a theoretical framework for exploring these interactions is indeed needed.

Our goal here is to develop a relatively simple discrete-generation model that describes the interactions between a local synchronous host/parasitoid system and an alternative, invasive and alien host, sharing the parasitoid with the local host. We focus particularly on the impact of the invader on the local community members when its seasonal cycle is synchronous or asynchronous with the local host–parasitoid system. Scenarios obtained by means of our description can be used for interpreting or predicting complex host/parasitoid dynamics in real ecosystems.

2. Modelling

Let us consider a pre-existing host/parasitoid system in which the two members are native and seasonally synchronized. Upon the arrival of an alien alternative host, this two-member interaction becomes a “shared enemy” community module (Holt, 1997). The alien host may or may not be seasonally synchronized with the native members. We also assume that there is no direct competition for resources between the two hosts.

To be concrete, the reader may, for example, think of two gall-making or leaf-mining insects as hosts, and an idiobiont parasitoid as the shared enemy. Consequently, the key life-cycle phases in which the interactions occur are the larval stage for the hosts and the adult female for the parasitoid. We thus describe the host populations as the numbers of larvae in the stage(s) suitable for enemy attack and the enemy as the number of adult females searching for hosts.

2.1. Seasonality

In our model, every generation of the native members comes after the previous one regularly, without any break. For narrative simplicity, the reader may think that both the local host and the parasitoid are multivoltine (having more than one generation per year), but they have the same number of generations per year. On the contrary, the alien host may be univoltine (having only one generation per year, see for a formal definition Tauber and Tauber, 1981). Thus, the alien host presents susceptible life stages in only a single generation, after which it enters dormancy and does not interact with the native members of system until the successive year. More generally, the susceptible life stages of the alien host appear only every τ (with $\tau \in \mathbb{N}^+$) generations of the local host (Fig. 1). In our context we define as seasonal synchrony as the simultaneous occurrence of the generations throughout the year. In contrast, “within-generation” synchrony denotes a situation in which the interacting life-cycle phases of the respective species occur simultaneously during each generation (in line with the use of the term “phenological synchrony” in, e. g., Miller-Rushing et al., 2010; Johansson et al., 2015) (Fig. 1). In order to isolate the effect of the seasonal asynchrony in our system, we assume that the “within-generation” interactions are perfectly synchronous.

2.2. Alien host density

The negative indirect interaction between two victim species that share a natural enemy is called apparent competition (– –) (Holt and Lawton, 1993). However, a number of empirical studies (Smith and Quin, 1996; Chaneton and Bonsall, 2000; Courchamp et al., 2000; Brassil and Abrams, 2004) show how the apparent competition is often an asymmetrical interaction very close to apparent amensalism (0 –), in which one victim is inhibited or eliminated while the other remains unaffected. Examples include cases in which an introduced prey population is resistant to high levels of predation (thanks to its own life history traits and/or behaviour) and, even if the new prey causes an increase in the predator population, it is, in turn, less proportionately affected. Immediately after their establishment, alien insects can reach high, invasive population densities. In the cases of leaf-mining and gall-making species, a quick shift of native parasitoids to the new alien host is regularly observed (for example Vercher et al., 2005; Girardoz et al., 2006; Schönrogge et al., 2006; Zappalà et al., 2012), but the native enemies are not able to impede significantly the growth of the invasive host (see for example Prior and Hellmann, 2013; Bürgi et al., 2015; Stacconi et al., 2015). Over time, this situation does not change and parasitoid richness shows only a slight tendency to increase (Cornell and Hawkins, 1993).

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