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Consequences of asymmetric competition between resident and invasive defoliators: a novel empirically based modelling approach

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Abstract

Invasive species can have profound effects on a resident community via indirect interactions among community members. While long periodic cycles in population dynamics can make the experimental observation of the indirect effects difficult, modelling the possible effects on an evolutionary time scale may provide the much needed information on the potential threats of the invasive species on the ecosystem. Using empirical data from a recent invasion in northernmost Fennoscandia, we applied adaptive dynamics theory and modelled the long term consequences of the invasion by the winter moth into the resident community. Specifically, we investigated the outcome of the observed short-term asymmetric preferences of generalist predators and specialist parasitoids on the long term population dynamics of the invasive winter moth and resident autumnal moth sharing these natural enemies. Our results indicate that coexistence after the invasion is possible. However, the outcome of the indirect interaction on the population dynamics of the moth species was variable and the dynamics might not be persistent on an evolutionary time scale. In addition, the indirect interactions between the two moth species via shared natural enemies were able to cause asynchrony in the population cycles corresponding to field observations from previous sympatric outbreak areas. Therefore, the invasion may cause drastic changes in the resident community, for example by prolonging outbreak periods of birch-feeding moths, increasing the average population densities of the moths or, alternatively, leading to extinction of the resident moth species or to equilibrium densities of the two, formerly cyclic, herbivores.

1. Introduction

Interspecific interactions act in unison with other factors in shaping species composition in ecosystems. Competition (in a broad sense) has been proposed as being one of the major forces defining the structure of various communities (Holt, 1977; van Veen et al., 2006). For herbivorous insect communities, the role of interspecific competition in defining species composition has been debated for several decades (Hairston et al., 1960; Connell, 1983). More recently, the importance of direct and indirect interspecific competition in structuring herbivore communities has become more clear (Harrison and Karban, 1986; Denno et al., 1995; Redman and Scriber, 2000; van Veen et al., 2006, 2009; Kaplan and Denno, 2007; Tack et al., 2009).

Invasive species entering a new environment are able to cause drastic changes in the invaded environment. Forest insect herbivores are known to be able to affect the invaded ecosystems particularly by altering interspecific interactions via trophic cascades (Kenis et al., 2009). Vice versa, a successful invasion of new insect species into a system is affected by interactions with competitors and natural enemies. Coexistence of an invasive and a resident species competing for resources has been extensively studied. According to classical theoretical work (MacArthur 1970; Schoener, 1974; Chesson, 2000), invasion and coexistence of two competing species is possible when intraspecific competition overrules interspecific competition. Predation, on the other hand, may hinder or stop the advancement of an invasion, if the invasive prey suffers from Allee effects at the range edge (Owen and Lewis, 2001). Then again, an invader can invade a system if specialist predators are not present, or if it can sustain higher levels of generalist predators than the resident species (e.g. Holt et al., 1994; Menéndez et al., 2008). The latter case of apparent competition arises through an indirect interaction between the two species mediated by the numerical response of a common enemy to the increased population density of the invader (Holt, 1977). The subordinate resident species may either be outcompeted from a location or evolve to utilize enemy-free space, in which case coexistence might be possible (see for example Ishii and Shimada, 2012).

When both resource and apparent competition take place in a community, coexistence is more likely, if the invader and the resident species show a trade-off in competitive ability and vulnerability to predation (Chesson and Kuang 2008). When higher competition ability affects fecundity or vulnerability to predation in a particularly asymmetric way, competition between species increases the probability of coexistence (Abrams, 1999; Nattrass et al., 2012; Heard and Sax, 2013). Indeed, combining resource competition and predation pressure, Chesson and Kuang (2008) showed that, coexistence is not likely, if species niches do not differentiate from each other and there is no trade-off between predation and competition. Furthermore, shared predation may also limit the range of coexistence of competing species when predation occurs on a geographical gradient (Holt and Barfield, 2009).

Furthermore, invasions are more probable in heterogeneous environments, whether the native community is biologically or temporally heterogeneous (reviewed in Melbourne et al., 2007). In temporally heterogeneous communities, where the more vulnerable prey competing with the invader exhibits cycles with the shared predator, the conditions for coexistence with the less vulnerable invader may be restricted (Abrams, 1999). In another study, Holt and Barfield (2003) found several possible outcomes for the range of species coexistence when a shared predator population exhibited temporal variation (Holt and Barfield, 2003).

Recently not only the effects of invaders on the interactions in a community but also the potential evolutionary effects of invasions on the resident community have come to broader attention (Sakai et al., 2001; Pintor et al., 2011; Jones and Gomulkiewicz, 2012). When evolution of the traits affecting competition and/or fecundity are under consideration, it has been found that 1) asymmetric competition may promote evolutionary branching between competing species in some cases (Kisdi 1999), 2) invasions of an alternative prey may destabilize the coevolutionary system between predator's attack ability and prey's defence (Mougi, 2010), 3) coexistence may be more restricted when evolution of consumer traits of resource choice instead of ecological consequences are considered (Egas et al., 2004) and 4) adaptation after invasion of a consumer into a system with competing consumer and a shared predator might promote coexistence (Abrams and Chen, 2002a).

Of the indirect mechanisms structuring terrestrial herbivore communities, apparent competition is a highly plausible, but little studied phenomenon (Morris et al., 2004, 2005; van Veen et al., 2006). In particular, surprisingly few studies have been made of apparent competition in the context of invasive insect species (Settle and Wilson, 1990; Redman and Scriber, 2000; Juliano and Lounibos, 2005; Kenis et al., 2009; Péré et al., 2010). Even fewer studies have looked at the evolutionary consequences of such interspecific interactions (Lau, 2012). As a consequence of apparent competition, the common natural enemy may, in some localities, cause the extinction of all but one species. This situation, termed dynamic monophagy (Holt and Lawton, 1993) may prevent observation of apparent competition (Holt and Lawton, 1994). However, invasions by non-native species into new environments create a stage for observing apparent competition before the ongoing interactions are obscured over time or by evolutionary changes in the community interactions.

A good example of an ongoing invasion, well suited for studying numerous ecological questions, is located in northern Fennoscandia. Here, the cyclic winter moth [Operophtera brumata L (Lepidoptera: Geometridae)] has recently extended its outbreak range to include parts of northernmost Finland and Norway (Hagen et al., 2007; Jepsen et al., 2008, 2009; Klemola et al., 2008). The invasion of this forest lepidopteran was likely promoted by warming temperatures due to climate change (Bylund, 1999; Jepsen et al., 2008, 2011; Ammunét et al., 2012). As a consequence of the invasion, the winter moth has already caused visible defoliation and tree deaths in its main host plant, the mountain birch [Betula pubescens ssp. czerepanovii (Orlova) Hämet-Ahti] in large areas far away from its earlier outbreak range (Tenow, 1972; Klemola et al., 2007, 2008; Jepsen et al., 2008, 2009). These areas were previously dominated by the autumnal moth [Epirrita autumnata (Borkhausen) (Lepidoptera: Geometridae)], which also feeds on the mountain birch. The 9–11-year population cycle of the autumnal moth is a well-studied phenomenon (Tenow, 1972; Lehtonen, 1987; Haukioja et al., 1988; Klemola et al., 2002), and recent empirical evidence suggests that parasitism by hymenopteran parasitoids is the driving agent in continental parts of the northern Fennoscandia, where winter moths have very recently spread (Klemola et al., 2008, 2010).

There the 9–11-year population cycles of the species have often been observed to be phase-locked, but with winter moth cycle phases lagging 1–3 years compared with those of the autumnal moth (Tenow, 1972; Hogstad, 2005; Tenow et al., 2007). These asynchronous population cycles have also been observed in the new area of sympatric occurrence, imposing almost continuous high defoliation pressure on the shared host plant (Fig. 1, Klemola et al., 2008, 2009). The continuous defoliation due to phase-lagged symmetric outbreak peaks rules out the possibility of the cycles being resource driven. Therefore, the interactions between the resident autumnal moth and the invasive winter moth have recently come under study with the aim of discovering which regulating agent might allow the two herbivore species, while sharing the same host, to cycle in an asynchronous way. Studies have been carried out concerning direct competition, apparent competition via shared host plant (Ammunét et al., 2010), and possible evolutionary effects through changes in host plant resistance (Ammunét et al., 2011). None of these interactions have been observed to be strong enough to drive such population dynamics.

As suggested by theoretical approaches (Abrams, 1999; Nattrass et al., 2012), asymmetric preferences of generalist predators and specialist parasitoids causing apparent competition are a plausible explanation for the coexistence of two cycling moths. In addition, apparent competition may act as an explanation for the phase-lagged cycles of the winter moth (Klemola et al., 2008, 2009). A strong preference of a shared natural enemy for one of the two moth species may suppress the densities of the preferred moth species and allow the densities of the other moth species to increase (Klemola et al., 2009). Generalist predators are likely to only affect the species in low population densities due to lack of strong numerical response or quickly saturating functional response to prey densities (Turchin, 2003; Heisswolf et al., 2009). Specialist parasitoids, however, are able to respond to high population densities (Berryman, 1996; Klemola et al., 2010) and affect the moth population dynamics to a large extent.

Recent studies have shown differences in the preference of specialist parasitoids and generalist pupal predators on the two moth species in the continental mountain birch ecosystem (Heisswolf et al., 2009; Klemola et al., 2009, T. Klemola, unpublished data). The parasitism rates and the diversity of the parasitoid assemblage seemed to be higher for autumnal moths than for winter moths (Klemola et al., 2009), at least locally and immediately after the density peak of the former species. In contrast, invertebrate pupal predators (such as beetles) seem to prefer winter moths over autumnal moths. Winter moth pupae have been observed to come under attack as much as three times more frequently than autumnal moth pupae (Heisswolf et al., 2009; Klemola et al., 2009, T. Klemola, unpublished data). Although parasitism and predation rates are known to differ and vary temporarily and geographically between the species (see for example Vindstad et al., 2010; Schott et al., 2012), it is likely that asymmetries in predator/parasitoid preferences are needed for the coexistence of the two similar moth species on longer time scale. Futhermore, although short-term apparent competition was not observed in the findings of the one-year study (Klemola et al., 2009), the asymmetric preferences of the predators may be reflected as long-term apparent competition between the two cyclic defoliators. However, due to the long periodic cycles for both of the moth species, an experimental approach to study the possible consequences of long-term effects of generalist and specialist predation, potentially leading to apparent competition, is challenging, requiring a study period of several decades. Thus, we present here a modelling approach to predict the consequences of the asymmetric effects of natural enemies.

In this paper we constructed a model with one or two host species (moths) and one parasitoid species using a Nicholson-Bailey type discrete-time host-parasitoid model. In order to take into account also the generalist predators, the model was split into two parts. We used empirical data from the autumnal and winter moth system in northern Fennoscandia as a guideline for the model construction and for the parameter values.

The two moth species were considered to diverge only in two parameters, s and m, depicting the effects of the asymmetric preference of the generalist pupal predators and the effects of the asymmetric preference of the parasitoids, respectively. By assuming a linear trade-off between the two parameters, the model depicts the effects of generalist predators and specialist parasitoids simultaneously on the population dynamics of the moth species.

Our first aim was to investigate how the observed asymmetric predation and parasitism preferences might affect the coexistence of the invader and the closely related resident autumnal moth. We first investigated the one host-parasitoid model and then performed an invasion analysis, calculating the invasion fitness (long-term exponential growth rate) of the species. Our second aim was to investigate, if long-term apparent competition could be observed for parameter combinations allowing for coexistence. In addition, we were interested in what consequences the asymmetries might have on the population dynamics of the moth species on an evolutionary time scale. As the invasion in the studied system is still a relatively new phenomenon, using the adaptive dynamics theory to investigate the evolving interactions between a resident and an invader brings us valuable information on the possible development of the invaded community. A similar approach has been previously suggested (Mooney and Cleland, 2001; Pintor et al., 2011), but we know of no other study that has applied this technique in order to study the consequences of an ongoing invasion.

2. Calculations

2.1 Empirical background

The autumnal and winter moths are univoltine, medium-sized (wingspread ca 3–4 cm), cryptic, forest-dwelling moths. Autumnal moth adults eclose from mid-August onwards and the males start to actively seek their less mobile mates. Winter moth adults eclose a couple of weeks later and the females are wingless. Females of both species lay eggs on tree trunks, branches and shoots, where the eggs overwinter. The foliage-feeding larvae emerge in the spring. The larvae experience five instars from late May to mid-July in northern Fennoscandia, and pupate in the soil.

The 9–11-year cycle of the continental autumnal moth populations seems to be driven by delayed density-dependent effects of hymenopteran parasitoids (Klemola et al., 2008, 2010) acting as facultative specialists in these areas with a low number of alternative hosts. In addition, winter moths seem to display population cycles with a period of 9–11 years in the original outbreak area (Tenow, 1972).

In previous sympatric outbreak areas, closer to the relatively mild coastal areas of northern Fennoscandia, the populations of the two moth species most often occupy areas at slightly different altitudes (Bylund, 1999; Hagen et al., 2007). Where the outbreak areas overlap, the asymmetric population dynamics of the two moth species can be observed (Figure 1). In the new area of sympatric occurrence winter moths share generalist predators and some of the specialist parasitoids with autumnal moths (Klemola et al., 2009, 2010). The parasitoid assemblage includes egg, early and late larval (both solitary: one new parasitoid emerges from the host and gregarious: several new parasitoids emerge from the host), and pupal parasitoids for both species.

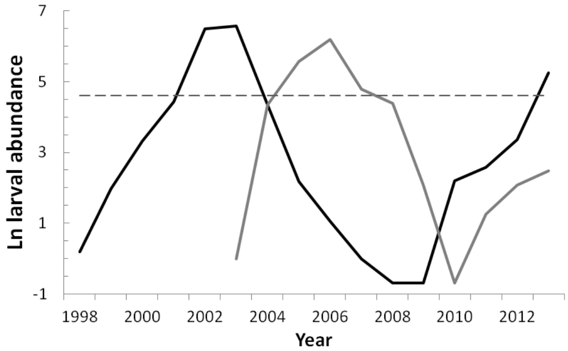

Figure 1. Field-collected larval abundance data (number of larvae in mountain birches per 10-min search) from the new sympatric area in northernmost Norway (Hana) where the invasive winter moth (solid gray line) noticeably entered the community previously dominated by the autumnal moth (black solid line) in 2003. The gray, dashed horizontal line marks the approximate larval abundance required to inflict visible defoliation on mountain birch, and can be considered to be the lower limit of an outbreak density. The data collection methods in Hana have been described by Klemola et al. (2008).

2.2 Population model

A two host-parasitoid Nicholson-Bailey type model split into two parts was constructed. The first part included asymmetric effects of generalist predators and the second part included the realized effects of parasitism. The aim was to answer our questions with a relatively simple model. Thus, the effects of the parasitoid guild are expressed by a single shared parasitoid that, for practical reasons, was assumed to be a solitary late larval endoparasitoid emerging as an adult the next year.

First, the endogenous population dynamics are described. Let $\mathrm{H}_{\mathrm{i}}^{\mathrm{t}}$ be the population size for moth species i at time t. The parameters for reproductive potential r, fecundity F ($F = e^r$), probability of survival c, and carrying capacity K were all obtained from previous studies of autumnal and winter moths (Haukioja et al., 1988; Tanhuanpää et al., 2002; Heisswolf et al., 2009; Klemola et al., 2009). In the earlier studies these parameters were not observed to undergo any major change in relation to species (Klemola et al., 2009), and were thus kept constant and equal for the two moth species in this study. The population size after reproduction, but before predation was assumed to be FcH_i^t.

Assume then a generalist predator attacking both species i and j, but preferring one of them when both are present. Parameter $\mathrm{s_i}$ depicts the relative efficiency of moth i to escape generalist predators. As generalists are less likely to have a numerical response to prey densities, predation depends solely on the moth population densities and has a direct effect on the prey population densities through r. When both prey species are present, the asymmetric preference of the predator, described by $\mathrm{s_i}$, results in “competition for enemy-free space” and is modelled with the function $\propto (\mathrm{s_i}, \mathrm{s_j})$. Accordingly, the population size of moth species i after generalist predation is assumed to be

$$\widehat{H}_i^t = FcH_i^t e^{\frac{-r\sum \propto (s_i, s_j) H_j^t}{K}}, \qquad \text{(Eqn 1)}$$

where the term $\sum \propto \left(\mathrm{s_i}, \mathrm{s_j}\right) H_j^t = \propto (\mathrm{s_i}, \mathrm{s_i}) H_i^t + \propto \left(\mathrm{s_i}, \mathrm{s_j}\right) H_j^t$ describes within species (first part) and among species (second part) competition. Assuming $\propto \left(\mathrm{s_i}, \mathrm{s_j}\right) = \propto (\mathrm{s_j}, \mathrm{s_i})$, when $s_i \neq \mathrm{s_j}$ would lead to symmetric competition. However, the parameter s is motivated by asymmetric competitive ability, thus the competition function is assumed to satisfy conditions $\propto \left(\mathrm{s_i}, \mathrm{s_j}\right) < \propto (\mathrm{s_j}, \mathrm{s_i})$, when $s_i > \mathrm{s_j}$. Within species competition is scaled to $\propto (\mathrm{s_i}, \mathrm{s_i}) = 1$, since predators are not assumed to follow individual prey species’ densities in a density dependent manner. In particular, we assume that $\propto \left(\mathrm{s_i}, \mathrm{s_j}\right) = \mathrm{e}^{-\gamma(\mathrm{s_i}-\mathrm{s_j}) - \xi(\mathrm{s_i}-\mathrm{s_j})^2}$ where $\gamma > 0$ and $\xi > 0$. Assuming $\gamma = 0$ would again lead to symmetric competition.

Second, we assume a parasitoid species attacking the hosts in the larval stages, but emerging only the following year. In addition, we assume that generalist pupal predators predate on parasitized and non-parasitized pupae indiscriminately. Therefore, the host-parasitoid dynamics take place after the prey-predator dynamics described above. Let P_t be the population size of parasitoids at time t. The probability of a moth escaping parasitism is assumed to be $e^{-m_i P_t}$ where m_i is the parasitism vulnerability on host species i. Therefore, moth population i after parasitism at time t+1 is

$$H_i^{t+1} = \widehat{H}_i^t e^{-m_i P_t}. \qquad \text{(Eqn 2)}$$

Further, the parasitoid population at time t+1 is

$$P_{t+1} = \widehat{H}_1^t (1 - e^{-m_1 P_t}) + \widehat{H}_2^t (1 - e^{-m_2 P_t}). \qquad \text{(Eqn 3)}$$

From the point of view of a moth, a minimal value of m and a maximal value of s would maximize reproduction. We assume that it is unlikely to achieve such values at the same time due to the opposing preferences of predators and parasitoids on the moth species. Without a trade-off in these parameters, it is unlikely that the two moth species would coexist (Abrams, 1999; Nattrass et al., 2012). The effects of predation as parameter s are thus depicted as a competition function in the first part of the model, and the effects of parasitism as parameter m are included in the second part. High values of s_i have positive consequences for the population densities of prey species i and high values of m_i have negative effects on the population densities of prey species i. Assuming from now on $s_i = m_i$ we implement the opposing asymmetric effects of generalist pupal predators and specialist parasitoids on the two moth species in one parameter. Overall, high values of m_i thus describe a high parasitoid attack rate and at the same time weaker effects of generalist predators on species i.

2.3 Modelling the invasion with adaptive dynamics framework

In the event of predators and parasitoids attacking two host species, the parameter m_i can be viewed as the moth vulnerability trait that is free to evolve due to learning and consequent change in predator/parasitoid preference (Ishii and Shimada, 2012). Thus, parameter m_i is referred to as “trait” from now on.

The invasion ability (i.e. invasion fitness) of species i with trait m_i in the environment set by species j was first investigated. The invasion fitness (long-term population growth rate) of the invader species (winter moth) with trait m_{inv} (diverging from m_{res}) in the environment defined by the resident herbivore E_{res}, is

$$r(m_{inv}, E_{res}) = ln\big(R(m_{inv}, E_{res})\big), \qquad \text{(Eq 4)}$$

where

$$R(m_{inv}, E_{res}) = \lim_{n\to\infty} \frac{H_{inv}^{n}}{H_{inv}^{0}} = \lim_{n\to\infty} \sqrt[n]{\prod_{t=1}^{n} Fce^{\frac{-\propto(m_{inv}, m_{res}) r H_{res}^{t}}{K} - m_{inv} P^{t}}}$$

$$= Fce^{\frac{-\propto(m_{inv}, m_{res}) r \overline{H}_{res}}{K} - m_{inv} \overline{P}}$$

It is assumed that the resident species (autumnal moth) is first at a positive population-dynamical attractor which can be a stable equilibrium or a cyclic orbit (Geritz et al., 1998; Parvinen, 1999; Doebeli, 2011). When the invasion fitness of the invader in the present environment is positive $r(m_{inv}, E_{res}) > 0$, the invader population may grow and invade the system (e.g. Metz et al., 1992; Geritz et al., 1998). The invader may become a new resident on its own, in which case it alone sets the environmental conditions. Alternatively, if the invasion fitness of the former resident m_{res} in the environment E_{inv} set by the former invader is positive, $r(m_{res}, E_{inv}) > 0$, these two traits are expected to coexist, in which case the new resident population consists of two traits. In any case, a new mutant may again have positive fitness in the present environment potentially resulting in further invasions. With small mutational steps taking place, the changes in species traits caused by these reciprocal mutation-invasion events define a trait-substitution sequence. The so formed selection gradient, that is defined as the derivative $\frac{\partial}{\partial m_{inv}} r(m_{inv}, E_{res})|_{m_{inv}=m_{res}}$, thus follows the evolution of a trait. Strategies, for which the selection gradient is zero, are singular strategies. If invasions of mutant strategies nearby the singularity all lead to the development of both resident and mutant strategy towards the singularity the singularity is an evolutionary attractor (Christiansen, 1991). A singular strategy is uninvadable, also called ESS-stable (Maynard Smith, 1958), if at the singular strategy $\frac{\partial^2}{\partial {m^2}_{inv}} r(m_{inv}, E_{res})|_{m_{inv}=m_{res}} < 0$. If an evolutionarily attracting singular strategy is not uninvadable, it is called a branching point

(Geritz et al., 1998). In this case the evolving trait m in the populations is expected to become dimorphic supporting two species i and j, and the two traits m_i and m_j are expected to evolve further apart from each other.

When calculating invasion fitness, it is enough to know the average densities of the populations instead of detailed knowledge of population densities of the resident moth H_{res}^{t} and parasitoid P^{t}. Small mutational steps are often assumed in the framework of adaptive dynamics when calculating invasion fitness (Metz et al., 1992, 1996; Geritz et al., 1997, 1998). While generalist predator and specialist parasitoid preferences can be subjected to evolutionary adaptation (Ishii and Shimada 2012), this assumption is valid also in our study system, although the invading moth species is coming from outside the system rather than developing from the resident species as a result of mutations.

3. Results and analyses

3.1 One host-parasitoid model

Population dynamics created by the one host-parasitoid model with respect to parameter m (Eq 1, 2 & 3) were studied from a phase plot (Figure 2). For small values of m, the parasitoid is not able to coexist with the moth. For intermediate values, they coexist in a stable equilibrium, and for larger values, coexistence occurs in a population-dynamical cycle (Figure 2). For values $m > 0.87$, the model produced extremely low parasitoid densities, which drove the dynamics down to zero as a result of computational inaccuracies. In reality, the remaining host population would eventually be parasitized again. Thus, for larger parameter m values, the model does not seem to describe natural populations sufficiently. Further analytical explorations of the one host-parasitoid model were restricted due to the exponential nature of the equations.

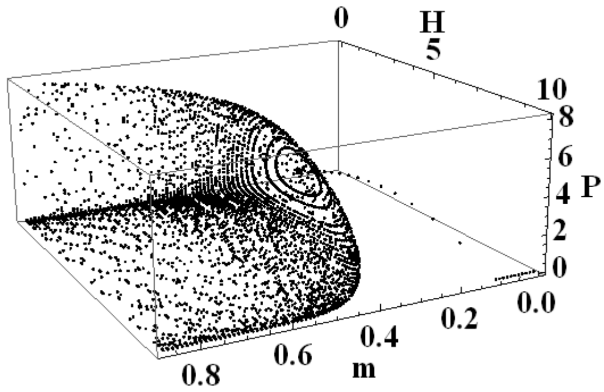

Figure 2. Population densities showed equilibrium and cyclic dynamics for herbivore (H) and parasitoid (P) in a one host-parasitoid system depending on the values of parameter m. Computational inaccuracies drove the parasitoid population down to zero at approximately $m > 0.87$. Model dynamics were calculated for the fixed parameters r = 1.55, F = 4.73, c = 0.5, K = 178 (larvae per 1000 short shoots).

3.2 Invasion and coexistence

The sign of the invasion fitness values (Eq 4.) for the two host-parasitoid system were calculated for all $(m_\mathrm{i}, m_\mathrm{j}) \leq 0.87$ and are illustrated in a pairwise invasibility plot (PIP, Figure 3A). The PIP shows (Geritz et al., 1998), that a singular strategy, which is a monomorphic attractor, but not evolutionarily stable, exists at approximately $m^* = 0.11$. Thus the population near the singularity, $m_{\mathrm{i,j}} \approx m^*$, becomes dimorphic. The singular strategy at $m^* = 0.6$ is repelling. With these parameter values, no other evolutionary attractors could be observed. Trait pairs, for which $r(m_1, E_2) > 0$ and $r(m_2, E_1) > 0$ define the area of mutual invasibility, i.e. the area where the competing host species coexist (Figure 3B; gray areas). Because the numbering of the trait is arbitrary, the area of coexistence is symmetric across the diagonal.

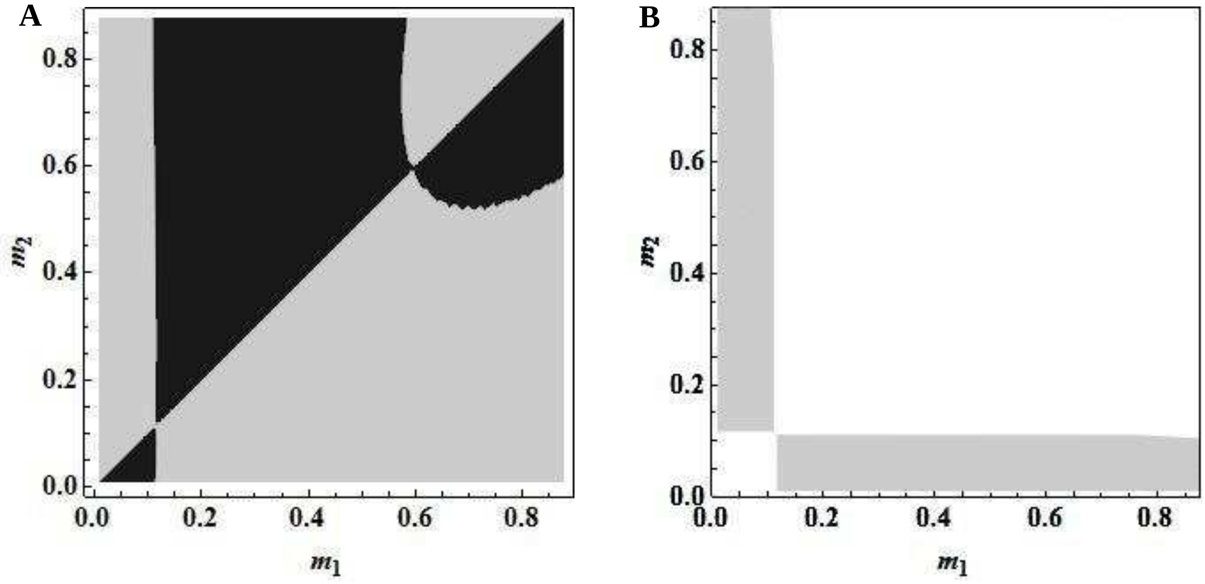

Figure 3. **A**: The pairwise invasibility plot shows the sign of the invasion fitness $r(m_{inv}, E_{res})$ of a rare trait m_{inv} in the environment set by the resident trait m_{res}. Black areas indicate negative invasion fitness and light gray areas indicate positive invasion fitness. Two singular strategies are found where the non-diagonal isocline crosses the diagonal, at approximately $m^* = 0.11$ and $m^* = 0.6$. The singular strategy at the smaller m value is evolutionarily attracting, but not uninvadable, and hence it is a branching point. The singular strategy at $m^* = 0.6$ is repelling. **B**: The parameter area for the strategy pairs of mutual invasibility, i.e. for coexistence, for which $r(m_1, E_2) > 0$ and $r(m_2, E_1) > 0$ is shown in gray. Model dynamics were calculated for the fixed parameters r = 1.55, F = 4.73, c = 0.5, K = 178 (larvae per 1000 short shoots), $\gamma = 2$, $\xi = 4$.

3.3 Evolutionary analyses

The found singular strategy at $m^* = 0.11$ is an evolutionary branching point. Further evolutionary analyses of the model were pursued in order to shed light on the possible long-term consequences of the invasion. The isoclines of the dimorphic selection gradient were first calculated (Figure 4, dashed line). Initially, the dimorphic strategy pair, (m_1, m_2), is near the branching point $m^* = 0.11$. By exploring the sign of the selection gradient in the dimorphic area of coexistence (see Kisdi, 1999; Kisdi et al., 2001 for more detailed description) indicating the expected direction of the trait substitution sequence, we see how the strategy pair then evolves on an evolutionary time scale (Figure 4, bold line and arrows). Although a singular strategy pair at approximately (0.01, 0.7) or (0.7, 0.01) exists, it can be seen from the phase-plane plot, that it is evolutionarily repelling. Thus, instead of approaching this point, the evolutionary changes drive the strategies out of the area of coexistence and one of the traits goes extinct. The evolution of the monomorphic trait, thus formed again, approaches then again the branching point $m^* = 0.11$ and the trait substitution sequence starts all over again. Thus, the evolutionary dynamics follow a so-called branching-extinction cycle (Kisdi et al., 2001; Dercole, 2003).

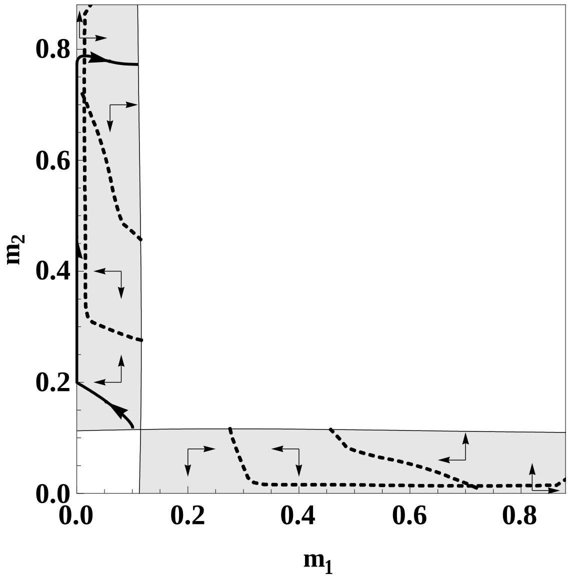

Figure 4. The parameter area for the strategy pairs of mutual invadability, for which $r(m_1, E_2) > 0$ and $r(m_2, E_1) > 0$, i.e. for coexistence, is shown in lighter gray. The isoclines for the dimorphic dynamics are shown with a dashed line, while smaller arrows show the direction of the selection gradient. The expected trait substitution sequence is indicated with a solid, bold black line with arrows. Model dynamics were calculated for the fixed parameters r = 1.55, F = 4.73, c = 0.5, K = 178 (larvae per 1000 short shoots), $\gamma = 2$, $\xi = 4$.

3.4 Statistical analyses

3.4.1 Population dynamics

Visual and numerical inspections of the population densities of all three species showed variation from constant to oscillatory dynamics with respect to the different combinations of (m_1, m_2) in the parameter area of coexistence through which the trait substitution sequence is moving on an evolutionary time scale (Figure 5A). Statistical auto-correlation function (ACF) - analysis (the ARIMA procedure in SAS 9.3 statistical software) for the time-series extracted from the model confirmed that most of the oscillatory dynamics are cyclic. The analysis was produced separately for the two host species for all trait value pairs $m_1 < m_2$ in the area of coexistence. Overall, cyclic dynamics involved approximately half (52%) of the possible parameter pairs. Cycle length for the moth populations varied from 11 to 27 years, increasing with the increasing values of m_1 and m_2 (Figure 5B). For the values $m_1 = 0.01$, $m_2 = 0.56$, for example, the three-species system produced approximately 16-year cycles for the moth species (Figure 6).

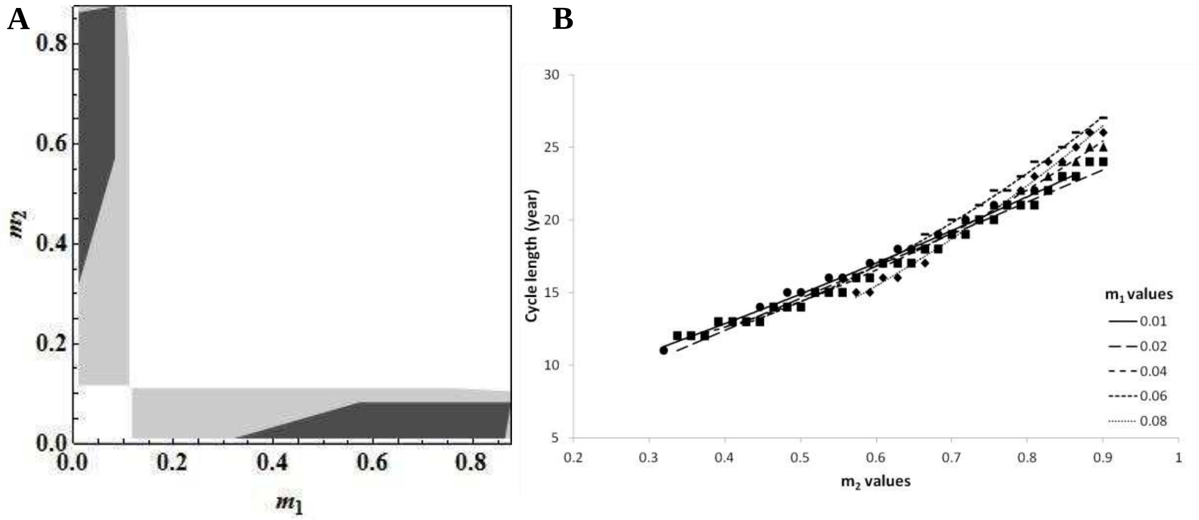

Figure 5. **A**: The area of coexistence of the two moth species is indicated by gray coloration. Coexistence in equilibrium is shown in lighter gray, while the darker gray areas show the oscillatory dynamics observed in the coexistence area. **B**: Cycle length for moth populations at different values of m_1 and m_2. Results were obtained from statistical auto-correlation function analyses. Both moth populations H1 and H2 had equal cycle lengths through values of m_1 and m_2.

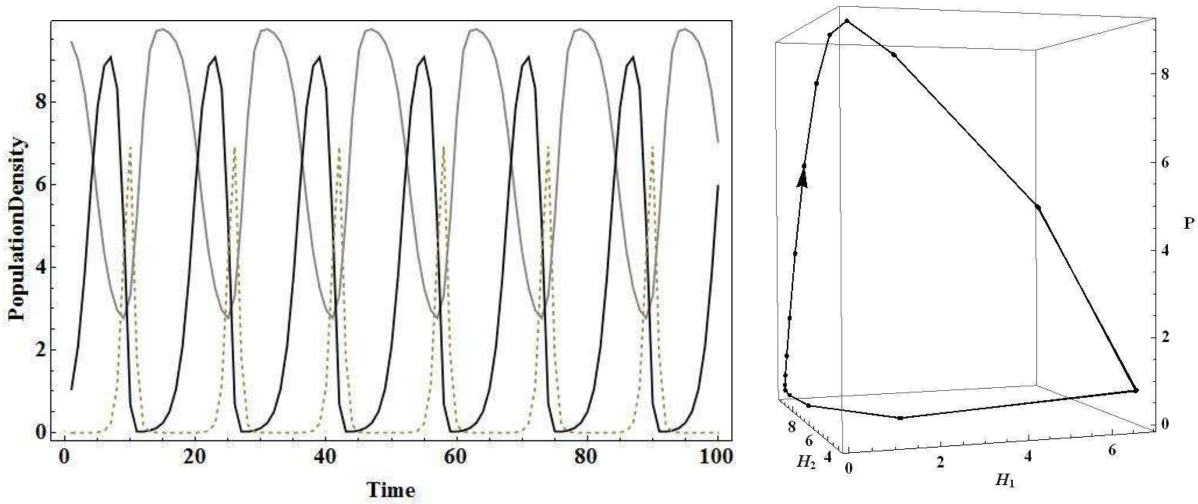

Figure 6. **On the left**: Population dynamics for two moths (gray and black solid line, H_1 and H_2) and a shared parasitoid (gray dashed line, P) with respect to time. The two moths cycle in 16-year periods in asynchrony, with approximately eight years between the peaks. **On the right**: The corresponding phase plot. The black arrow shows the direction of the cycle. The trait values are $m_1 = 0.01$, $m_2 = 0.56$. The constant parameters are the same as in Figure 2.

3.4.2 Asynchrony

The cyclic dynamics were explored in more detail in order to see whether asynchronous population dynamics may be caused by the asymmetries in parasitoid preference and in the effects of generalist predators on the moth species. The model-produced time series was analysed for the relationship between the two moths and between the parasitoid and moth population fluctuations by cross-correlation-function analysis (CCF, run with the ARIMA procedure in SAS 9.3).

The lag between the significant positive correlations between the different moth species (H1 vs. H2) varied from 4 to 8 years, with an increasing trend with increasing m_2 at lower $m_1$values (Figure 7A). The increasing trend in the number of years between the correlations was diluted with increasing values of m_1 (Figure 7A). As an example, the highest correlation for parameter values $m_1 = 0.01$, $m_2 = 0.56$ was seen with a lag of 5 years between the populations (Figure 7C). Similar increasing trend between lag years and values of m_2 was seen when cross-correlating the parasitoid population with each of the moth species (Figure 7B). The parasitoid population correlated most with a 3-10 year lag behind moth population H2 and 7-19 years behind moth population H1, depending on the values of m_1 and m_2. The increase in the lag values was of approximately the same magnitude for all parameter m_1 values. However, the number of lag years was constantly smaller for moth species H2 than moth species H1, corresponding to the order in which the three species built up to peak densities in the model (Figure 7B). For example, the parasitoid population had a lag of 4 years to moth H2 whereas best correlation with moth H1 was found at a lag of 9 years at parameter values $m_1 = 0.01, m_2 = 0.56$ (Figure 7D).

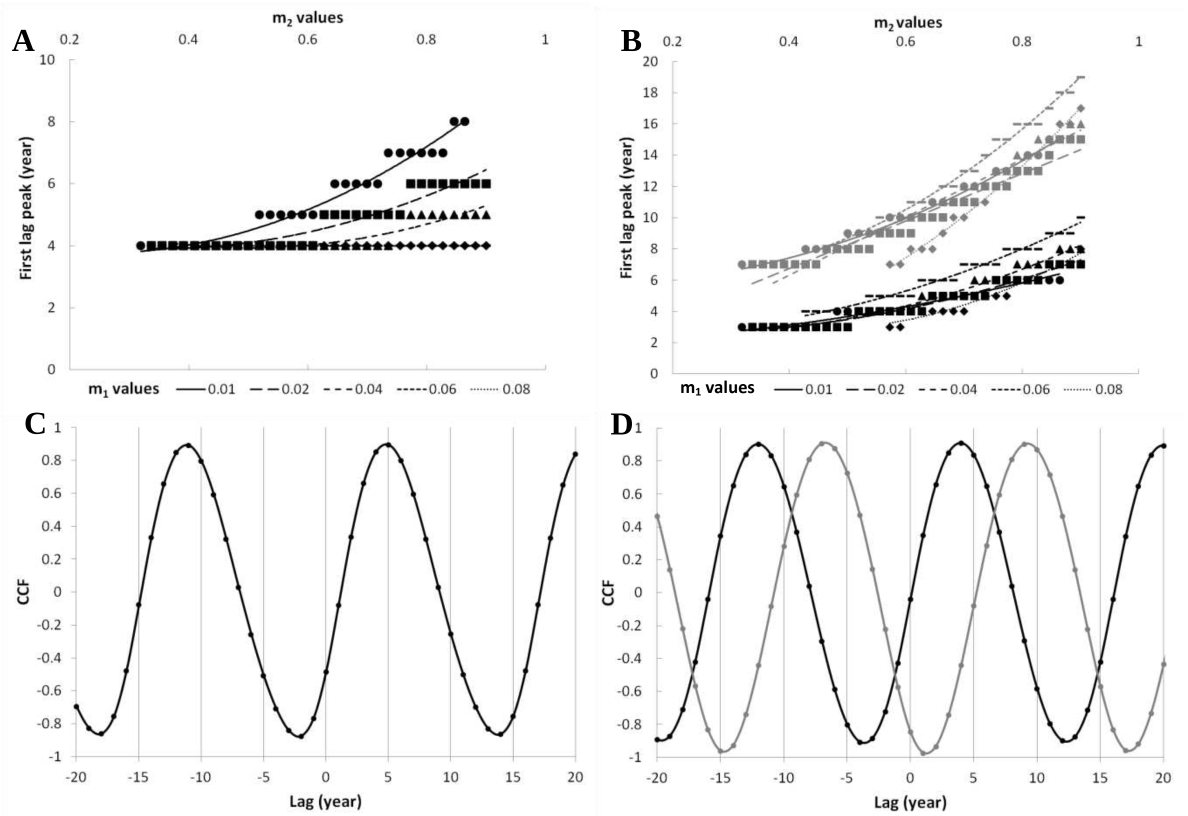

Figure 7. **A**: Number of lag years for correlation between H2 and H1 populations in relation to values of m_1 and m_2. **B**: Number of lag years between correlations of parasitoid population with H1 (light gray) and H2 (black) moth populations in relation to values of m_1 and m_2.**C**: Cross-correlation function results for the correlation between the two moth species for parameter values $m_1 = 0.01, m_2 = 0.56$. Correlation was highest at a lag of 5 years. **D**: Cross-correlation function results for the correlation between the parasitoid population and H1 (light gray) and H2 (black) for parameter values $m_1 = 0.01, m_2 = 0.56$. Correlation

between the parasitoid population and H1 and H2 was highest for a lag of 9 and 4 years, respectively.

3.5. Realized effects of apparent competition

The average population densities of the resident moth species seemed to have a declining trend with increasing values of m_1 and m_2, whereas the average population densities of the invader increased slightly (Figure 8A). In order to study the realized indirect effects of apparent competition of the invasive species on the resident population, the average population density of the herbivore species in a one host-parasitoid situation, $\overline{H}(m_1)$, was compared to the average population density of the respective species in a two host-parasitoid situation, $\overline{H}_1(m_1, m_2)$. Across the parameter area of coexistence, in the context of a large fraction of the trait value pairs, the invasion of the second herbivore species had positive effects on the average population density of the resident herbivore species, irrespective of the underlying population dynamics (Figure 8B).

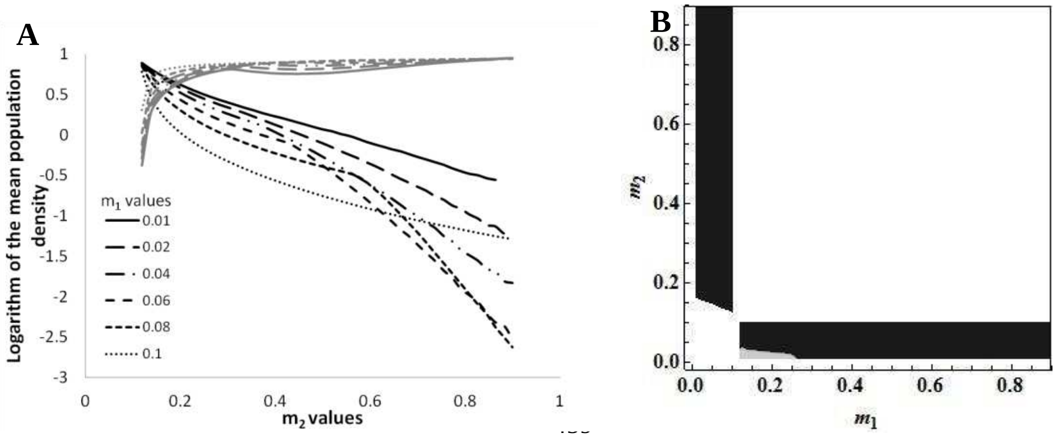

Figure 8. **A:** Logarithm of the mean population densities for moth species H1 (gray) and H2 (black) across different values of m_1 and m_2, where $m_1 < m_2$. **B:** The realized effects of apparent competition between the resident and the invasive moth species. The trait values(m_1, m_2), for which the average population density of the herbivore species in one host-parasitoid situation, $\overline{H}(m_1)$, is greater (light gray) or smaller (black) than the average population density of the respective species in a two host-parasitoid situation, $\overline{H}_1(m_1, m_2)$. The fixed parameters are the same as in Figure 2.

4. Discussion

4.1 Invasion and coexistence in a system with competing resident species and a shared parasitoid

According to our model, the invasive winter moth was able to invade a community with a resident autumnal moth competing for enemy-free space and sharing parasitoids. In addition, the invader was able to attain a positive long-term population growth in the newly invaded community. The invasion was possible when the resident community was at a point with relatively low specialist parasitoid pressure reflecting earlier theoretical and experimental findings for invasive species (Holt and Lawton, 1994; Shea and Chesson, 2002; Menéndez et al., 2008). In addition, temporal variation, such as the cyclic dynamics in our modelled resident community, is in general, thought to increase possibilities for new invasive species to enter (Chesson, 2000; Shea and Chesson, 2002; Melbourne et al., 2007).

In general, relatively higher reproductive rate in the invading species has been thought to enable invasion into a system where the resident species has lower reproductive rate (Holt and Lawton 1994). In our model the resident and invasive moth species had equal reproductive rates, as observed in experimental studies (Kaitaniemi et al., 1999; Heisswolf et al., 2009; Klemola et al., 2009). In the model, as in nature, both moth species were also assumed to have relatively high reproductive rates. Therefore, differences in reproductive rates do not act as an explanation for the invasion in our model. However, as the reproductive rate must be high enough in relation to predation or parasitism in order for a species to invade, the generally high reproductive value with low parasitism rates may have partly aided in the invasion of the winter moth (Holt, 1977; Holt and Lawton, 1994).

At the point of parameter values allowing invasion, divergence occurred for trait m depicting asymmetric preference of generalist predators and specialist parasitoids, and dimorphic coexistence of the invader and resident moths was observed for a restricted area of parameter values. The area of coexistence was observed only when the values of m were pronouncedly asymmetric in relation to the two moth species. That is to say, the trade-off between vulnerability to generalist pupal predation and parasitism was pronounced. Nattrass et al. (2012) showed that the probability of coexistence for competing species increases with increasing asymmetry in fecundity/competition trade off, with a relatively similar sized area of coexistence (Figure 3B). Likewise, other similar constrains for coexistence have been shown theoretically (Law et al., 1997; Abrams, 1999; Abrams and Chen, 2002a, 2002b, Chesson and Kuang 2008) and experimentally (Heard and Sax, 2013) between species competing for resources and sharing predation pressure in the community.

In addition to differences in the relative growth rates of the prey species, coexistence is usually dependent on the numerical response of the consumer (Holt and Lawton, 1994). The parasitoid population here responded to host density in a simple way without density dependence in the attack rate or limitation in the number of eggs. As argued before, it is not probable that the functional response would have changed population dynamics significantly and thus generated a higher possibility of coexistence for the two moth species (Holt, 1977; Abrams, 1999). However, the functional response of the parasitoid may have been slightly too simplified in our model as it follows the moth densities without a limited number of eggs or density dependent attack rate and, in being so, it drove the dynamics to zero due to computational inaccuracies when parameter values for m were higher than 0.87. More information on the behaviour of the parasitoids in the northern system would be required in order to estimate the parasitoid functional response more accurately.

Generalist predators, included in the competition function describing the outcome of the asymmetric effects of generalist predation (Heisswolf et al., 2009; Klemola et al., 2009), acting on prey populations are thought to promote the coexistence of competing species, when the dominant competitor is more affected by predation (Hanski et al., 1991; Chase et al., 2002). This reflects the requirement of a trade off between competition and predation required for coexistence without niche divergence (Chase and Kuang 2008). We did not compare the size of the coexistence area with and without the asymmetric effects of generalist predation, and hence no conclusion can yet be reached as to whether generalist predation would promote coexistence by itself in our study system. On the other hand, empirical evidence exists on persisting coexistence of the two moth species even without significant differences in parasitism rates (Schott et al., 2010). This may indicate the importance of asymmetric generalist predation preferences in the northern system allowing for species coexistence.

4.2 Ecological and evolutionary consequences

The inherent oscillatory nature of insect herbivore-natural enemy dynamics seems to have obscured the comprehensive studying of the effects of apparent competition in these systems (Morris et al., 2005). Negative long-term effects were not inflicted on the average population densities of the resident species by the invader in our model. On the contrary, according to our modelled dynamics, invasion of the winter moth into the mountain birch ecosystem promoted higher average densities in the resident species (Figure 8B). Previous studies have reported that, when the parasitoid preference towards two hosts is not equal, the interactions often have positive effects on the less vulnerable species and negative effects on the more vulnerable species (Brassil and Abrams, 2004). Although this did not seem to be the case in our modelled system, the average population densities of the resident moth species had a general declining trend with increasing values of m (Figure 8A).

Furthermore, apparent competition via differences in parasitoid preference in addition to the asymmetric effects of generalist predators produced asynchronous cycles for the two sympatric moth populations. Cycles were observed in more than 50% of the dynamics observed from the parameter area of coexistence. The moth density peaks, following one another by a few years, create a prolonged defoliation pressure on the shared host, in comparison to pre-invasion situation, as has also been observed in nature (Figure 1, 6). In addition to the effects of prolonged defoliation, the relatively longer defoliation pressure due to outbreaks of two species following each other could expose the mountain birch forests to further threats, such as pathogens (Ahlholm et al., 2002; Ammunét et al., 2011).

The modelled cycles were most similar with the observed data in parameter value pairs with large differences. This fits well with the proposed idea that the parasitoids and predators should act almost in a specialised way in order to produce the asynchronous cycles observed in nature (Klemola et al., 2008, 2009). These observations are in accordance with previous studies that have shown that switching and learning of shared natural enemies may promote coexistence and create asynchronous cycles in shared host species (Abrams and Kawecki, 1999; Ishii and Shimada, 2012).

Our modelling effort suggested that asymmetric effects of predation and parasitism alone are able to produce a lagged synchrony in the shared host moth species. However, the cycle length in the modelled dynamics with two moth species was similar to the observed cycles only at low parameter values of $m_1(0.01 - 0.02)$ and $m_2(0.3 - 0.4)$. In addition, the observed 2-year lag between the moth peaks seemed to be constantly overestimated by our model, which suggested that the moth populations are most similar with a lag of 4-8 years. These inaccuracies between the modelled and observed dynamics may be explained by other exogenous and intrinsic factors, besides parasitism and predation, operating and/or regulating the dynamics of the natural populations. Abiotic factors, food quality (and quantity in outbreaks) and density dependent intrinsic mechanisms, for example, may affect the realised peak densities as well as the rate of decline at the post-peak phase of the cycles in the mountain birch forests (Tanhuanpää et al., 2002). Furthermore, the observational data on the asynchronous cycles comes from a relatively short period of time compared to the cycle lengths of the moth populations, which makes the comparisons between the model and the observations problematical.

In nature, it seems that the autumnal moth reaches its high density populations first, followed by the winter moth (Tenow 1972, Figure 1). Based on our model results, the order of the moth population peaks cannot be deducted in a straightforward manner. Depending on the parameter values, the number of years between the peaks of both moth populations were equally spaced or nearly equally spaced (data not shown). For example, the populations in figure 6 each have a 16-year cycle, with one moth population following the other by 8 years. In such cases, it is not possible to say which moth population precedes the other.

On the other hand, half of the model parameters in the area of coexistence generated stable or dampening population dynamics and also the near extinction of the preferred species was observed (Figure 8A). These dynamics have also been reported in previous studies describing populations with apparent competition (Brassil and Abrams, 2004). The modelled stable dynamics may be expected if the presence of each host in the asynchronous cycles maintains the parasitoid densities when the other host goes through a low density phase (Brassil and Abrams, 2004). Furthermore, the effects of generalist predators, depicted in the form of the competition function, have likely affected the interaction between the competing host species and a shared parasitoid (Holt and Lawton, 1994; Abrams and Chen, 2002a), thus resulting in stable or dampening dynamics.

Overall, generalist predators acting on prey populations are thought to dampen the cyclic dynamics of competing species, when the dominant competitor is more vulnerable (Hanski et al., 1991; Chase et al., 2002). In our system, winter moths seem to suffer from a higher pupal predation rate probably due to higher vulnerability of smaller-sized pupae (Heisswolf et al., 2009; Klemola et al., 2009, T. Klemola, unpublished data). Nevertheless, cycles were observed in more than half of the dynamics in the parameter area of coexistence, thus showing no signs of the damping effect of predation on cyclic, competing prey populations in half of the parameter values. Generalists may also have promoted the asynchrony in our study system, since there is indication, that in the coastal areas the parasitism rates for the two moth species are very similar, but still cycles following each other by two years exists (Schott et al., 2012).

It has been reported that cyclic dynamics often dampen the effects of apparent competition (Abrams et al., 1998), which might also be the case here. Nevertheless, it seems that the invasion promoted not only subsequent peaks in defoliating moth species populations, but an overall increase in the long term average of the population densities of the resident moth species. In addition, cyclicity in the resident community may have increased the potential for evolutionary diverging strategies (Geritz et al., 2007), enabling the coexistence of the two modelled species.

In addition to cyclicity on an ecological timescale, evolutionary dynamics of the combined dimorphic trait m showed cyclic changes within the area of coexistence. These branching-extinction cycles drive the development of the trait from monomorphic to dimorphic, eventually driving one of the traits to extinction and back to a monomorphic trait again (Kisdi et al., 2001). These fluctuating evolutionary dynamics may be caused by the cyclic population dynamics in the ecological time scale (Khibnik and Kondrashov, 1997). The branching-extinction cycle might also reflect the tight coupling of parasitoids to the two moth populations that are able to drive the population densities to extremely low levels. However, this remains to be analytically shown.

The invasion of the winter moth in our model seems to maintain temporal heterogeneity in the populations and in addition induce evolutionary heterogeneity in the invaded system.

The added heterogeneity in the northern system may promote further invasions (Melbourne et al., 2007) and therefore increase the probability of changes in these communities.

4.3 Conclusions

To conclude, the modelling approach, using adaptive dynamics framework, revealed possible outcomes of the ongoing invasion that would otherwise have been difficult to observe because of cyclic dynamics with a long cycle period. Invasion and coexistence of a competing species sharing parasitoids with the resident was possible with pronouncedly asymmetric parameter values. The model was able to produce somewhat similar dynamics to those pertaining between the two moth species in nature. Although the short-term effects of asymmetric predation and parasitism preferences could not be observed in nature over the course of a single study year (Klemola et al., 2009), the long-term effects seemed to be positive on the resident species in the parameter area under investigation, most likely increasing the defoliation pressure on the shared host plant. In sum, this study represents an example of potential indirect effects of an invasive species on the resident community (Kenis et al., 2009). However, the modelled dynamics were not evolutionarily stable, with the alternatives being equilibrium densities for the moth and parasitoid species and even extinction of the preferred moth species following branching-extinction cycles. This implies that the observed asynchronous cycles may not persist over an evolutionary time-scale, but drastic changes in the community may be inflicted by the invasive moth species.

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