



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



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HIGHLIGHTS

- We used empirical data to model long-term consequences of invasion.
- Asymmetric predation and parasitism rates for resident and invader were modelled.
- Evolutionary consequences were analysed using the framework of adaptive dynamics.
- Model supported previous hypothesis about the causes of observed asynchronous cycles.
- Modelling revealed possible drastic changes inflicted in the invaded ecosystem.

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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.

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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

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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; Natrass 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; Natrass 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.

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