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Entomopathogenic fungi and invasional meltdown

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Invasive non-native (alien) species are considered to be one of the greatest threats to biodiversity (Millenium Ecosystem Assessment 2005) through predation, competition, hybridisation or as vectors of disease (Hulme *et al.*, 2009). The movement of peole and goods is increasing the rate of invasive alien species arriving in countries around the globe. A recent inventory of alien species in Europe revealed a figure of 11000 species (Hulme *et al.*, 2009) but it is recognised that this is a first approximation and likely to be an underestimate (Olenin & Didžiulis, 2009). The distinction between native species and alien species is problematic; species have been moving around the world over millennia and the origin of many species is uncertain. It is also evident that many archaeophytes and archaeozoans establish within native communities without detrimental effects on species and ecosystem processes (Pyšek *et al*., 2005). However, the small proportion of alien species that are problematic (invasive) are both ecologically and economically costly (Hulme *et al.*, 2009). Furthermore, historically species movements have occurred within continents but in recent decades an increasing proportion of alien species are from other continents (Hulme *et al.*, 2009). Alien species originating from within a continent are predicted to be less invasive than those from other continents (Hulme *et al.*, 2009).

The term "invasional meltdown" describes the process by which an alien species facilitates invasion by another alien species by increasing the likelihood of survival and / or the magnitude of impact of the alien species (Simberloff & Von Holle, 1999). So essentially "invasional meltdown" is used to describe synergistic interactions among invasive alien species which lead to accelerated impacts on native ecosystems. However, it is a concept that is difficult to explore because, although many studies have examined individuals of one species providing a benefit to the establishment and spread of another, there is a scarcity of information on population impacts. The introduction of the yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island and its interactions with native and alien scale insects is considered to have led to major disruption (possibly replacement) of the native food web essentially invasional meltdown (O'Dowd *et al.*, 2003). The ants feed on native red crabs (*Gecarcoidea natalis*) and dramatically reduce the crab population. The ground cover plants, which the crabs usually feed on, increase in abundance and density. The populations of native and alien scale insects increase because the ants protect them from predators. Consequently honeydew, secreted by the scale insects, increases as the number of scale insects increase and this results in the growth of sooty mould. Canopy die back is attributed to the prolific growth of this sooty mould on foliage within this disrupted system. The complex set of interactions, leading to the so-called invasional meltdown on Christmas Island, requires understanding of the intricacies of the yellow crazy ant food web.

Understanding the interactions between invasive alien species and other species, within an invaded range, is challenging but essential, particularly for quantifying effects on communities. It is possible to envisage the effects of an alien species on a spectrum from negligible effects to dramatic disruption of species, communities and ecosystem processes. A number of studies have assessed the infiltration of alien species into a community using food web analysis (Henneman & Memmott, 2001; Memmott and Waser, 2002; Sheppard *et al.*, 2004). Sheppard *et al.* (2004) examined the interactions between alien predators, introduced to Hawaii to control pest insects, and endemic invertebrates (mainly Lepidoptera) within pristine upland habitats. Approximately 11 % of the predators within the food web were alien to Hawaii (Sheppard *et al.*, 2004). The findings of Henneman & Memmott (2001) were dramatic; 83 % of Lepidoptera parasitoids, in a native forest on Kauai Island (Hawai), were alien species introduced as biological control agents and a further 14 % were accidentally introduced adventive wasps (only 3 % of the parasitoids were native). The construction of food webs provides intriguing insights into alien species but the absence of invertebrate pathogens in such studies is notable.

The main focus of research on alien species within food webs has centred on alien predators released as biological control agents. Therefore, it is, perhaps, surprising that invertebrate pathogens have not been integrated into such studies, given their role as biological control agents. Most research on the interactions between alien species and fungal pathogens involves the evaluation of fungal pathogens as potential biological control agents of alien insect species which are causing damage to crops in North America. For example, *Beauveria bassiana* (Ascomycota: Hypocreales) has been explored for the control of diamond-back moth, *Plutella xylostella* (Lepidoptera: Plutellidae) (Vandenberg *et al.*, 1998) and the emerald ash-borer, *Agrilus planipennis* (Coleoptera: Buprestidae) (Liu & Bauer, 2008). *Metarhizium anisopliae* (Ascomycota: Hypocreales) and *Beauveria brongniartii* (Ascomycota: Hypocreales) have been assessed for control of the cirus longhorn beetle, *Anoplophora glabripennis* (Coleoptera: Cerambycidae). Seven species of entomopathogenic fungi were found infecting soybean aphids, *Aphis glycines* (Hemiptera: aphidae) including six Entomophthorales (*Pandora neoaphidis*, *Conidiobolus thromboides*, *Entomophthora chromaphidis*, *Pandora* sp., *Zoophthora occidentalis*, *Neozygites fresenii*) and one Hypocreales (*Lecanicillium lecanii*).

There is one insect that is considered an invasive alien species in many countries (Brown *et al.*, 2008) across three continents (Europe, North and South America and Africa), *Harmonia axyridis* (Coleoptera: Coccinellidae). This charismatic ladybird is a top-predator within the aphidophagous guild; a community which comprises both native and non-native species. It is native to Asia but has been introduced as a biological control of pest insects (principally aphids but also coccids) in Europe and America. It poses a threat to biodiversity because it is a polyphagous and voracious predator. In Britain there have been field reports of *H. axyridis* consuming moth (Lepidoptera: Noctuidae) eggs and the immature stages of native ladybird (Coleoptera: Coccinellidae) species. Interactions between fungal pathogens and this invasive alien species have been considered (Cottrell & Shapiro-Ilan, 2003; Roy *et al*., 2008a; Roy *et al.* 2008b; Steenberg & Harding, 2009). Field studies in Denmark demonstrated the susceptibility of *H. axyridis* to three hypocrealean fungal entomopathogens: *Isaria farinosa*, *B. bassiana* and species of *Lecanicillium*. Indeed, winter mortality due to fungal infection reached 17.9% in adults collected at one location (Steenberg & Harding, 2009). *Harmonia axyridis* also interacts with the aphid-specific pathogen *P. neoaphidis*. Roy *et al*. (2008b) demonstrated the role of *H. axyridis* as an intra-guild predator of *P. neoaphidis* infecting pea aphids. However, *H. axyridis* increases the transmission of this fungus between hosts (Wells *et al.*, in press). These studies highlight the potential of using *Harmonia axyridis* as a model species for examining the effects of an invasive alien species on food web dynamics, including insect pathogens.

Harmonia axyridis is widely accepted as posing a threat to native biodiversity and as such has the potential to disrupt food webs (Majerus *et al.*, 2006; Roy and Wajnberg, 2008). There has been considerable research on the interactions between this invasive alien species and other species within the aphidophagous guild. Our understanding of the interactions between *H. axyridis*, other predators, parasites and pathogens, could be modelled within a food web structure to provide further predictions on the impact of this species. Could *H. axyridis* also provide insights on invasional meltdown?

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