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European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America

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Abstract We consider the possibility of an extensive invasional meltdown occurring in central North America involving eleven Eurasian species. The scenario begins with the potential co-facilitation between the European earthworm *Lumbricus terrestris* and European buckthorn, *Rhamnus cathartica*. Once introduced, European buckthorn has served as the overwintering host for two important invasive crop pests, oat crown rust, *Puccinea coronata* and the soybean aphid, *Aphis glycines*. The spread of *R. cathartica* itself may have been aided by seed dispersal by the European starling, *Sturnus vulgaris*, and the presence of *L. terrestris* has likely facilitated the invasion of *Bipalium adventitium*, an Asian predatory flatworm that specializes on earthworms. Beyond this, the soybean aphid is consumed by a number of introduced species, including the lady beetle *Harmonia axyridis*, the ground beetle *Agonum muelleri* and the parasitoid *Aphelinus certus*. We hypothesize that the presence of soybean aphid increases regional abundances of these species. We discuss both the evidence for this multi-species invasional meltdown scenario and potential implications of meltdown dynamics for invasive species management. The particular management issues that we discuss are: (1) opportunities for managing multiple invasive species simultaneously by targeting facilitator species, and (2) implications of meltdown dynamics for biological control introductions against the soybean aphid.

Keywords Invasional meltdown · *Lumbricus terrestris* · *Rhamnus cathartica* · *Aphis glycines* · *Puccinia coronata* · *Harmonia axyridis* · *Sturnus vulgaris* · *Bipalium adventitium* · *Agonum muelleri* · *Aphelinus certus* · *Binodoxys communis*

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Introduction

Simberloff and von Holle ([1999]) introduced the term 'invasional meltdown' to describe situations in which

'a group of nonindigenous species facilitate one another's invasion in various ways, increasing the likelihood of survival and/or of ecological impact.' They classified interactions among nonindigenous species gleaned from 254 articles published in the ecological literature between 1993 and 1997 as either +/+, +/0, +/− or −/−, in which the two interaction directions apply reciprocally to two species (Abrams 1987). Out of 190 interactions between pairs of introduced species, 10 were interpreted by Simberloff & von Holle as being reciprocally facilitative (+/+). One-way facilitation (+/− or +/0 interactions) was found in 178 of the 190 interactions, with most of these being herbivory (+/−), in which an introduced plant facilitated an introduced herbivore. Richardson et al. (2000) have discussed plant invasions involving mutualistic interactions with introduced pollinators, seed dispersers, mycorrhizae, or nitrogen-fixing bacteria, although quantifying the importance of mutualisms between alien species was beyond the scope of their review.

Despite the initial focus on pairwise species interactions, Simberloff (2006) added that meltdown should be considered a 'community-level phenomenon in which the net effect of facilitations would lead to an increasing rate of establishment of introduced species and/or an accelerating impact'. In this vein, Ricciardi (2001) argued that a series of interrelated invasional meltdowns were occurring among introduced species in the Great Lakes of North America. And as we will discuss in more detail for our study system below, it has been suggested that introduced earthworms facilitate the establishment of introduced plants and other invaders, and in turn that introduced plants facilitate earthworm invasions, leading to the potential for positive feedback among invaders (Aplet et al. 1991; Kourtev et al. 1999; Frelich et al. 2006).

In this contribution we consider a series of interactions among invasive species in the North-Central United States that appear to fit the invasional meltdown model. The web of interactions that we consider is pictured in Fig. 1 and it is centered on the European shrub *Rhamnus cathartica* (common buckthorn) and the Asian soybean aphid (*Aphis glycines*) in the sense that these species are involved in the most direct interactions with other species in the web. The interactions that make up the putative extensive invasional meltdown can be summarized as follows:

(1) The growth and spread of *R. cathartica* is facilitated by the actions of invasive earthworms, in particular the European *Lumbricus terrestris*, and *R. cathartica* in turn creates favorable conditions for growth and reproduction of *L. terrestris*.

(2) Native earthworms are not present in the northern portion of the central United States, so that introduced earthworms such as *L. terrestris* facilitate the spread of the introduced Asian flatworm, *Bipalium adventitium*, a specialist predator of earthworms.

(3) *R. cathartica* is an important overwintering host of oat crown rust, *Puccinia coronata*, and has enabled the invasion of this plant pathogen. Cultivated oats, *Avena sativa*, also facilitated this invasion because they are a major host of oat crown rust during the summer growing season.

(4) *R. cathartica* is also an obligate overwintering host for the Asian soybean aphid, *Aphis glycines*, in the North-Central United States and thus enabled its invasion, as did widespread planting of soybean, the obligate summer host of *A. glycines*.

(5) The seeds of *R. cathartica* are dispersed by a number of bird species, including the European starling, *Sturnus vulgaris*, so starlings may have contributed to the spread of *R. cathartica* within North America. It is not clear whether feeding on *R. cathartica* berries improves or decreases starling fitness.

(6) A number of introduced predatory insects feed upon the soybean aphid in North America. In particular, populations of the invasive lady beetle, *Harmonia axyridis*, appear to be benefiting from the introduction of the soybean aphid. The introduced ground beetle *Agonum muelleri* has also been documented feeding on soybean aphids in the eastern US. Finally, an Asian parasitoid of soybean aphid, *Aphelinus certus*, appears to have been introduced either at the same time as the aphid or later.

Of the eleven species involved in this web of interactions, two are introduced crop plants (soybeans and oats), three are intentionally introduced species that have become invasive (*R. cathartica*, *S. vulgaris*, and *L. terrestris*) and five are accidentally-introduced invaders (*B. adventitium*, *Aphis glycines*, *P. coronata*, *Agonum muelleri* and *Aphelinus certus*). The eleventh species, *H. axyridis*, was both intentionally and accidentally introduced, and it is not clear which class of introduction has led to establishment and spread (see below).

Fig. 1 Schematic illustrating potential components and linkages of the extensive invasional meltdown discussed in the text. Lines with arrows indicate a positive effect in the direction of the arrows and lines with circles indicate negative effects in the direction of the circle. Thickness of lines is roughly proportional to the known or suspected strength of the interaction. Signs and magnitudes of arrows were derived from literature cited and discussed in the text. The sketches were composed by Julie Martinez
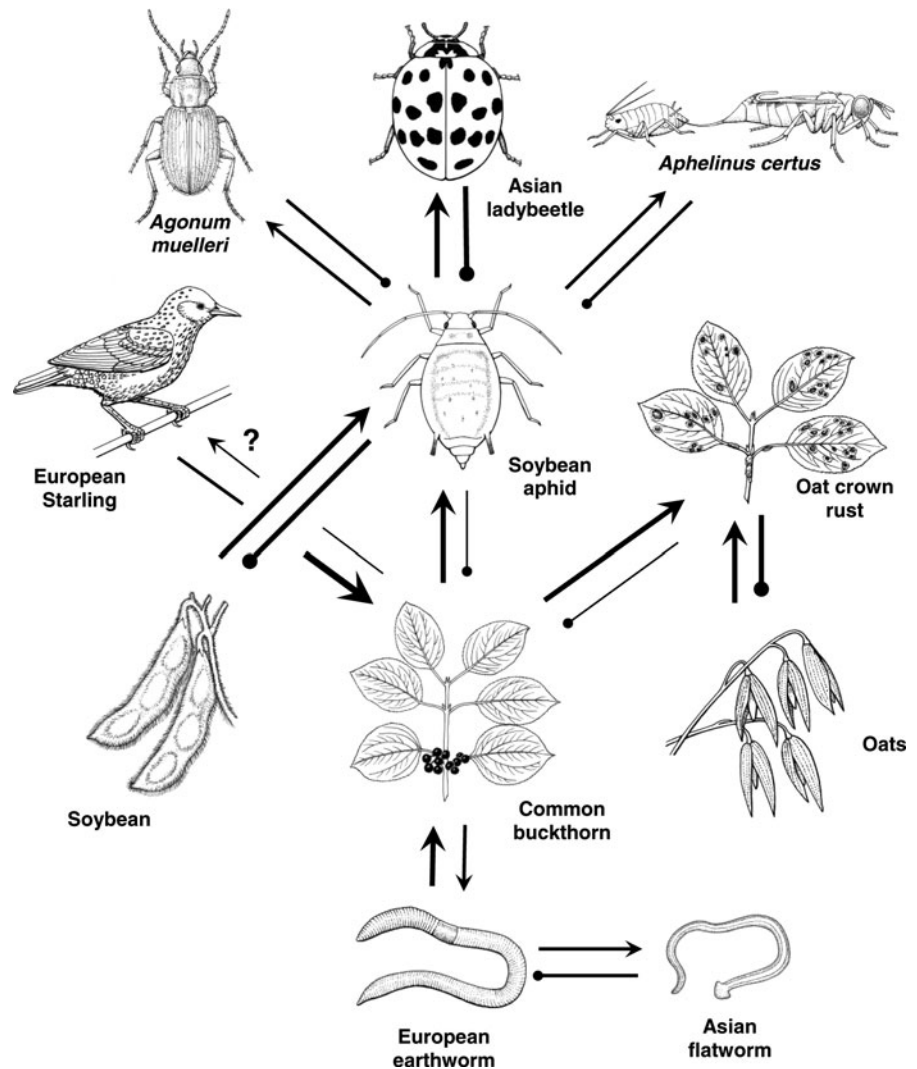
We begin by considering each interaction in turn to evaluate the evidence for or against meltdown dynamics, focusing in particular on evidence for facilitation at the population level. Where appropriate, we suggest critical tests that could be done to validate or disprove the hypothesis of facilitation. We then discuss implications of meltdown dynamics for invasive species management, focusing on European buckthorn and the soybean aphid, which has emerged as the most important pest of soybeans in North America since its detection in the year 2000 (Ragsdale et al. 2004). Our main purpose here is to articulate new hypotheses that are consistent with facilitation and invasional meltdown. Many of these hypotheses are currently untested and many of the linkages that we discuss are based upon fragmentary evidence. It is our hope that rigorous tests of the hypotheses that we pose for this set of interactions, and also for other similar interaction webs, be conducted in the near future.

Buckthorn, earthworms and starlings

Common buckthorn, *R. cathartica*, was introduced to North America by the early nineteenth century as a plant for use in hedges, and it continues to be used in this capacity on farms and residences to this day. However, it has escaped cultivation into fencerows, abandoned farmland, fallow fields and woodlands. It is especially abundant in oak woodlands that are

common in central and eastern North America. In the United States, several states list *R. cathartica* as a noxious, invasive, banned or prohibited weed (USDA Plants Database 2008). The question that we address here is—to what extent can this spread be attributed to introduced earthworms and, to a lesser extent, starlings?

Invasive earthworms and buckthorn

The landscapes in and around farms in the soybean belt of the North Central US have been extensively invaded by European earthworms (family Lumbricidae; James and Hendrix 2004). The northern portion of the soybean belt does not have native earthworms, so that European earthworms are the only species present, and although the southern portion of the soybean belt does have native earthworm species in the families Acanthodrilidae and Sparganophilidae (Hendrix 1995), European earthworms generally predominate over native earthworms in areas disturbed by humans, including the vast majority of farmlands in the central US (Butt et al. 1999). Asian earthworms in the genus *Amynthas* (family Megascolecidae) that have become established on the east coast are still rare in the central US (Reynolds et al. 2002, LE Frelich, unpublished data). The common suite of European earthworms found in agricultural and adjacent woodland settings includes three angleworm species (*Aporrectodea tuberculata*, *A. trapezoides*, and *A. turgida*), the field worm species *Octolasion tyrtaeum*, the leaf worm *Lumbricus rubellus* Hoffmeister and the nightcrawler, *L. terrestris*). The first five of these species are the preponderant earthworms in agricultural fields, while *L. terrestris* does not thrive in tilled fields due to lack of fresh litter, sensitivity to pesticides, and physical injuries from tillage (Kladivko et al. 1997; Butt et al. 1999).

In fencerows and woodlands however, *L. terrestris* often dominates the soil faunal community (Hale et al. 2005; Holdsworth et al. 2007). This species appears to have strong facilitative interactions with European buckthorn. Buckthorn leaf litter has ideal physical and chemical properties, including high nitrogen and calcium content, lack of tannins, and relatively soft leaves that are easy for earthworms to consume. These properties make buckthorn an excellent food source for *L. terrestris*, better than the sugar

maple and oak leaf litter commonly available in woodlands, and equal to the litter of native tree species with the highest quality leaf litter such as American basswood (*Tilia americana*) (Holdsworth et al. 2008). A buckthorn understory in the forest provides much more shade and cooler soil (preferred by *L. terrestris*) than would occur in the absence of buckthorn. Experimental removal of *R. cathartica* from 10 m^2 plots in southern Wisconsin led to a 63% decrease in earthworm abundance (likely dominated by *L. terrestris*) in the year directly following removal (Madritch and Lindroth 2009). Similar results were obtained by the same authors for the removal of Bell's honeysuckle, *Lonicera x bella*, another invasive shrub. This shows that *R. cathartica* is not the only exotic plant capable of facilitating earthworm invasions in North America.

In turn, *L. terrestris* recycles the nutrients in buckthorn leaf litter and provides a bare mineral soil seedbed that enhances germination and survival of buckthorn seedlings (Heneghen et al. 2007; Knight et al. 2007). Buckthorn seedlings find the floor of earthworm-free forests hostile because of a high density of tree seedlings and herbaceous plants and an O-horizon leaf litter that is normally 10–15 cm thick. Earthworm invasion, in combination with deer overabundance, reduces the density or sometimes eliminates native herbaceous and tree seedling plant cover (Frelich et al. 2006), leaving a vacant niche for invasive plant species (Frelich et al. 2006; Hale et al. 2006). In addition, the type of mycorrhizae that infect buckthorn roots are apparently not negatively affected by *L. terrestris* as are mycorrhizae needed by some native tree species (e.g. sugar maple, *Acer saccharum*) (Lawrence et al. 2003). The apparently mutualistic relationship between *R. cathartica* and *L. terrestris* is not surprising given that they evolved together in Europe.

Although there is no doubt that European buckthorn and *Lumbricus* change ecosystem properties to facilitate each other, the evidence that earthworm presence is necessary for buckthorn invasion, is circumstantial. No experiments have been done to explicitly test for differences in buckthorn germination, growth and survival in forests with versus without earthworms. There are, however, many welldocumented study sites with earthworms and no *R. cathartica*, but none with *R. cathartica* and no earthworms (Hale et al. 2006; Holdsworth et al. 2007,

LE Frelich unpublished). In contrast, the native buckthorn species *R. alnifolia* has been found in sites without European earthworms (LE Frelich, unpublished).

A critical test of the meltdown hypothesis for earthworms and buckthorn would involve long-term, field-scale manipulations to compare buckthorn germination with and without earthworms and also manipulations to compare earthworm reproduction and population growth with and without buckthorn. At this time, there are no proven management techniques to remove earthworms from large areas that would not also affect non-target organisms. And even if such a method were available, it is not clear how fast the ecosystem would return to its original state. This is particularly important as earthworms act on the germination and seedling survival phases of the *R. cathartica* life cycle, so that the existing adult plants would live out the rest of their lifespan of several decades.

The currently invading Asian flatworm *B. adventitium* is an exclusive earthworm predator and it would presumably not be present in the North-Central US were it not for the presence of introduced earthworms such as *L. terrestris*. It has been found in several states within the US (IL, OH, WI; Watermolen and Fojut 2008) but further research is needed to evaluate implications of the introduction of this species in both natural and agricultural areas, including whether it has the potential to reduce populations of *L. terrestris*.

Buckthorn and European starlings

It is well known that the seeds of Rhamnaceae are dispersed by birds in their native Europe (Ridley 1930; Godwin 1936), although *R. cathartica* in particular is suspected of being distasteful to many bird species, and European starlings are not among the German and British records of dispersers of this species (Woodruffe-Peackock 1918; Godwin 1943). Despite this, Lindsey (1939) found that *R. cathartica* berries comprised 8.3% of the stomach contents of European starlings during the month of November in New York in the early 1930s. Howell and Blackwell (1977) suspected that starlings were responsible for the spread of the closely-related *Frangula alnus* (syn. *Rhamnus frangula*; glossy buckthorn) into Ohio since both of these invasive species appeared in Ohio in the early 1920s. Working in Canada, however, Catling and Porebski (1994) noted that *F. alnus* invaded Ontario before starlings did, and that a number of native birds (in addition to starlings) fed on *F. alnus* fruits.

The information on the association between starlings and *Rhamnus* spp. suggests that these birds may have played a role in the spread of *R. cathartica* in some areas, although the role has likely been minimal in others, particularly given that native North American bird species are known to disperse *R. cathartica* seeds (Knight et al. 2007). Also not known is whether buckthorn fruits are a high-quality food for starlings or not. *Rhamnus* fruits are notorious for their strong purgative qualities and so may even be toxic. On the other hand, starlings are able to tolerate various poisonous substances and may benefit from feeding on buckthorn fruits (Howell and Blackwell 1977).

Buckthorn and oat crown rust

Oat crown rust, *P. coronata*, is an important pathogen of cultivated oats, *Avena sativa*, that is native to Europe and Western Asia. *P. coronata* can overwinter on various species of *Rhamnus* in both its native and introduced ranges, but its major overwintering host in North America is *R. cathartica* (Simons 1985). Oat crown rust occurs far outside the area where *R. cathartica* has invaded (Leonard 2003), so local populations of this overwintering host are clearly not necessary for rust development. Within the range of *R. cathartica*, however, infected oat fields do tend to be near *R. cathartica* stands (Chong et al. 2008). The critical questions concerning the importance of buckthorn in the distribution and pest status of oat crown rust in North America include: (1) whether species other than *R. cathartica* serve as overwintering hosts, and (2) whether reproduction on buckthorn is necessary to continue the life cycle of the pathogen. While *R. cathartica* appears to be the major overwintering host, it is not clear how critical the overwintering stage is for the overall life cycle. Roelfs (1989) discussed 3 forms of inoculum for cereal rusts in crops. The first are the sexually-produced aeciospores, generated on non-cereal overwintering hosts like *R. cathartica*. The second are windborne uredospores that overwinter on the cereal itself in areas warm enough for both the cereals and the uredospores (which are not produced sexually) to

overwinter. The third are uredospores from mycelia on grasses, which may originate from a number of sources, including non-crop grasses. For oat crown rust, it is generally assumed that aeciospores from *R. catharctica* form the bulk of the inoculum in areas where *R. catharctica* is widespread, including the North-Central United States and Southeastern Canada. Evidence for this is the observations that infected oat fields are often near buckthorn stands (Chong et al. 2008) and that infections often show signs of recent sexual reproduction (Groth and Roelfs 1982; Chong and Kolmer 1993; Chong et al. 2008).

McCallum et al. (2007) also suggested that *R. catharctica* contributes strongly to the ability of oat crown rust to counter resistance genes deployed in cultivated oats. Sexual reproduction of the rust occurs on buckthorn, and the abundance and widespread distribution of this overwintering host could allow for the emergence of novel virulence strains through recombination. Indeed, resistance to oat crown rust in oats is notoriously short-lived in North America (Leonard 2003; Chong and Zegeye 2004; McCallum et al. 2007), which itself suggests that overwintered aeciospores from *Rhamnus* are an important inoculum (Leonard 2003). This also suggests that suppression of *R. catharctica* could decrease virulence of oat crown rust even if it did not decrease its overall incidence.

Buckthorn and soybean aphid

The soybean aphid, *A. glycines*, was recently introduced from eastern Asia into North America and has invaded most soybean regions in the United States and Canada (Venette and Ragsdale 2004). In China, soybean aphid rarely reaches damaging levels on soybean (Wu et al. 2004b), but in North America, it has become a major pest of this crop (Ragsdale et al. 2004, 2007). Although soybean aphid has become the most important insect pest on soybean in Midwestern states, it has not become a major pest in mid-Atlantic or Southern states that have been colonized by this species.

Here we will concentrate on the hypothesis that facilitation by *R. catharctica* explains why soybean aphid is a major pest in the Midwest but not Asia or in the mid-Atlantic US. This hypothesis stems from the observation that the overwintering hosts of *A. glycines*—especially *R. catharctica*—are abundant in the Midwest but not in Asia or the mid-Atlantic

US. In Eurasia, the eastern distribution limit of *R. catharctica* is reached in the northwestern corner of China, where neither soybeans nor soybean aphids occur. Soybean aphid overwinters on other *Rhamnus* species (Wu et al. 2004b) in eastern regions of Asia. These *Rhamnus* spp. are not as abundant in Asia as *R. catharctica* has become in the Midwest (K Wu, K Hoelmer, KR Hopper and GE Heimpel, unpublished) and this may partially explain the low prevalence of soybean aphid there.

In North America, several *Rhamnus* species are the dominant if not sole overwintering hosts of soybean aphid, although there has been a report of reproduction on horsenettle, *Solanum carolinense*, in autumn (Clark et al. 2006). *R. catharctica* is the most widespread *Rhamnus* species north of the 41st parallel (Ragsdale et al. 2004; Voegtlin et al. 2005; Bahlai et al. 2007; Welsman et al. 2007). Soybean aphid is also able to overwinter and reproduce in the spring on the native North American species *Fragula alnus* (=*R. alnifolia*) and *R. lanceolata* (Voegtlin et al. 2005; Yoo et al. 2005), but there is no evidence that these native species contribute significantly to soybean aphid populations. *F. alnus,* may be marginally suitable as an overwintering host, but the oviparae do not survive to reproductive age on this host (Yoo et al. 2005). *Rhamnus davurica* has been introduced into North America from Asia, and has been widely planted as an ornamental, but is much less common in unmanaged habitats than *R. catharctica*; we are aware of no tests of the suitability of this species as an overwintering host for soybean aphid in North America, but soybean aphids have been observed overwintering on this species in Eastern Pennsylvania, USA.

In the mid-Atlantic states, where soybean aphid is at worst an occasional minor pest, *R. catharctica* and *R. davurica* are recorded from the Piedmont region in disturbed habitats such as old fields and field edges, roadsides and ditches (McAvoy and Bennett 2001). A substantial area in this region has been set aside in parks and other natural areas and this habitat is interspersed with agricultural production with soybean and corn being the dominant crops. Surveys in 2005 showed that *Rhamnus* species are rare in Delaware (McAvoy and Bennett 2001) but are more common in neighboring states and farther north, including New York State (Nielsen and Hajek 2005).

Soybean aphid was first detected in the US in Wisconsin in 2000 and outbreaks on soybean

occurred there and in neighboring states in the same year. The aphid was found in Pennsylvania and Virginia in 2001, Delaware in 2002, and Maryland in 2003 (Venette and Ragsdale 2004), but it has not reached outbreak levels in this region. Soybean aphid is not listed as a soybean pest by Extension on-line websites maintained by the University of Delaware, University of Maryland or the Virginia Polytechnic Institute. Surveys in a test plot of soybeans near Newark, Delaware during 2005 and 2006 failed to detect any immigrant alate aphids, and soybean aphids were not found until mid-season, and then at very low densities. For example, transect counts of *A. glycines* conducted in mid-September 2006 before crop senescence showed an average of 3 ± 4 aphids per trifoliate (mean $\pm$ SD, $n = 160$ plants).

As an indirect test of the hypothesis that aphid abundance on *Rhamnus* determines colonization of soybean and subsequent damage, we compared the control effort against soybean aphid, as measured by the percentage of soybean acreage treated with insecticide in a state (USDA-National Agricultural Statistics Service [www.nass.usda.gov], Agricultural Chemical Usage Field Crops Summaries for 2004–2006; and unpublished data from a survey for 2003), to the percentage of counties where *R. cathartica* was reported in that state (USDA-Natural Resources Conservation Service, National Plant Data Center, Plants Database [www.plants.usda.gov]). We concentrated on available data from states in the North-Central US, rather than in the Southeast, since virtually all insecticide use on soybeans in the North-Central US is directed at soybean aphids. We used data for treated soybean acreage from nine US states starting in 2003 (when soybean aphid had established in much of its current range in North America) and ending in 2006 (the last year for which data were available). We conducted a multiple regression analysis for the effects of year (a measure of time since soybean aphid was introduced), percentage counties with *R. cathartica* (a measure of *R. cathartica* abundance), and total soybean acreage on the percentage acreage treated with insecticide (an index of soybean aphid abundance). Percentages as proportions were arcsin-squareroot transformed to normalize distributions; analysis with a generalized linear mixed model assuming a gamma distribution for the percentage treated acres gave the same results so we report here only the general linear model results.
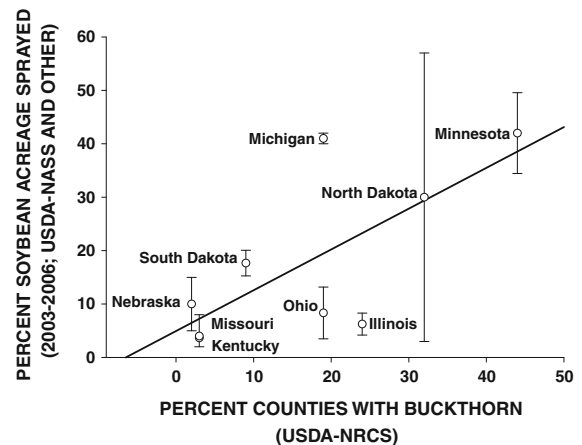
Fig. 2 Percent soybean acreage sprayed with insecticide versus percent counties with *Rhamnus cathartica*. *Bars* are standard errors of the means. See text for description of analysis

Percent soybean acreage treated with insecticide in a state did indeed increase with percent counties with *R. cathartica* ($F = 13.9$; $df = 1$, 18; $P = 0.002$; Fig 2), as well as with the total acreage of soybean in a state, although the effect for the latter was much weaker ($F = 4.1$; $df = 1$, 18; $P = 0.06$). Percent acreage treated did not vary with year ($F = 0.7$; $df = 3$, 18; $P = 0.58$) when the other variables where included in the model. A model that included *Rhamnus* abundance and soybean acreage alone explained 51% of the variance in percent soybean acreage treated with insecticide. The increase in percent acreage treated with total soybean acreage suggests that more soybean habitat increases soybean aphid reproduction per unit area of soybean habitat. This might arise from reduced mortality of soybean aphid during dispersal or from a reduced impact of natural enemies immigrating into soybean from other habitats. This analysis no doubt underestimates the effect of *R. cathartica* on problems with soybean aphid because the data set does not include mid-Atlantic states (where both soybean aphid and *R. cathartica* are rare), for which data on insecticide use on soybean or *R. cathartica* distribution or both are lacking. Still, it provides preliminary support for the hypothesis that the abundance of *R. cathartica* leads to higher soybean pressure on a per-state basis.

Of course, other (non-exclusive) hypotheses could explain regional differences in the pest status of soybean aphid. One of these is that natural enemies

have a greater impact on soybean aphid populations in China and the mid-Atlantic states than in the Midwest, particularly when the aphid is on *Rhamnus* spp. In China and the Eastern United States, both generalist predators and more specialized parasitoids are important (van den Berg et al. 1997; Liu et al. 2004; Wu et al. 2004b; Miao et al. 2007; Nielsen and Hajek 2005; Hajek et al. 2007; Wu, Heimpel and Hopper, unpublished data; see below). In the North-Central US, however, parasitoids have little impact on *A. glycines* (Lin and Ives 2003; Rutledge et al. 2004; Costamagna and Landis 2006; Kaiser et al. 2007; Noma and Brewer 2008; Noma et al. 2010) and at least one predator that is present in Eastern N. America (*A. muelleri*) is absent from soybean fields (see below). In Asia, parasitism rates ranging between 45 and 52% were routinely recorded over a 5 year period in Jilin province (Gao 1994), one of the principal soybean producing areas. Enclosure experiments in China also demonstrated that parasitoids can limit soybean aphid populations (Miao et al. 2007). Substantial parasitoid species diversity and parasitism rates have also been found during ongoing exploration for soybean aphid parasitoids in China and Korea, and parasitized aphids were routinely found whenever aphids were located (K Hoelmer, unpublished). Other hypotheses involve differences in climate, agricultural practices or cultivars of soybean, as well as landscape-level habitat differences that could interact with natural enemy impact (Gardiner et al. 2009a, b; Noma et al. 2010).

Critical tests that could be used to test the hypothesis that soybean aphid abundance is linked to local or regional *Rhamnus* abundance could include landscape-level analyses that seek spatial correlation between buckthorn and soybean aphid outbreaks. Indeed, Bahlai et al. (2008) have shown that soybean aphid density is positively correlated to the density of *R. cathartica* plants in the vicinity of soybean fields in Ontario, Canada. Another approach could involve experimental removal of *Rhamnus* stands in the vicinity of soybean fields. As discussed above, Madritch and Lindroth (2009) have used this general approach to assess the effect of buckthorn and honeysuckle on earthworm abundance. Similar studies could be done in the vicinity of soybean fields to test the hypothesis that buckthorn affects population dynamics of soybean at a very local scale.

Soybean aphid and its exotic consumers

The soybean aphid is consumed by a number of both native and exotic predators, parasitoids and pathogens in North America (e.g. Rutledge et al. 2004; Mignault et al. 2006; Nielsen and Hajek 2005; Costamagna et al. 2007, 2008). We discuss here three exotic species that have been documented attacking the soybean aphid—the multicolored Asian lady beetle, *H. axyridis*, the ground beetle *A. muelleri*, and the parasitoid *A. certus*.

Harmonia axyridis. The multicolored Asian lady beetle, *H. axyridis*, is a predator of the soybean aphid in both the aphid's native and introduced ranges (Liu et al. 2004; Wu et al. 2004a; Rutledge et al. 2004). While other exotic lady beetles such as *Coccinella septempunctata* and *Propylea quatordecempunctata* feed on soybeans in North America as well (see refs. cited above), we focus on *H. axyridis* as an exemplar of these ladybeetles because *H. axyridis* appears to be the most important species in terms of abundance and effects on soybean aphids themselves. *H. axyridis* (hereafter *Harmonia*) has been introduced into the US on multiple occasions via intentional release and possibly accidental transport. It was intentionally introduced into California as early as 1916 and again during the 1970s and 1980s for biological control of pear psylla (Gordon 1985). Between 1978 and 1981 it was introduced for biological control of pecan aphids in the southeastern US (Koch 2003). In spite of these early attempts at introduction, the first recorded establishment of *Harmonia* in the US did not occur until 1988 in southeastern Louisiana (Chapin and Brou 1991). It is speculated that this may have been due to accidental introduction via shipping (Day et al. 1994). Thereafter, *Harmonia* gradually spread throughout much of the US and southern Canada (Koch 2003).

Along with other predators, *Harmonia* provides a valuable ecosystem service in the form of biological control of the soybean aphid (Costamagna et al. 2007; Chacon et al. 2008; Gardiner et al. 2009a). Unfortunately, it has negative impacts as well. It is a strong intraguild competitor and has been implicated in the decline of several species of native lady beetles (Koch 2003; Harmon et al. 2007). Moreover it has become a significant economic and environmental pest in its own right, contaminating wine grapes, entering human dwellings in search of overwintering

sites, causing human allergies (Goetz 2008), and negatively impacting non-target insects (Koch et al. 2003; Koch and Galvan 2008).

Harmonia was well-established in the North Central US by the late 1990s, and thus preceded the first detections of the soybean aphid in 2000. However, several factors suggest that the arrival of the soybean aphid facilitated the further invasion and spread of *Harmonia*. First, *Harmonia* is one of the most commonly-reported natural enemies of soybean aphid, attacking it throughout its invasive range. Second, soybean aphid is an excellent prey species for *Harmonia*, resulting in high rates of reproduction. Finally, in long-term studies, populations of *Harmonia* appear to increase substantially following the introduction of soybean aphid, with some evidence that populations of both invaders are cycling in a classical predator–prey fashion. Here we explore these factors in further detail.

Harmonia, along with the native minute pirate bug, *Orius insidiosus*, is consistently among the most abundant natural enemies of *A. glycines* in North American soybean fields (Fox et al. 2004; Rutledge et al. 2004; Costamagna et al. 2007; Mignault et al. 2006; Donaldson et al. 2007; Chacon et al. 2008; Gardiner et al. 2009a, b). *Harmonia* appears particularly well-adapted to preying on soybean aphid. Costamagna et al. (2007) reported that of the 12 taxa observed to attack soybean aphid in a Michigan soybean field, only *Harmonia* adults exhibited a significant positive correlation with aphid density. In addition, they were among the most efficient predators on a per-capita basis. Mignault et al. (2006) found that *Harmonia* comprised up to 20% of the total foliar predators in Québec soybean fields. When fed a diet of *A. glycines* alone, *Harmonia* had the highest fecundity and intrinsic rate of increase of the three coccinellids tested indicating high prey suitability (Mignault et al. 2006).

An examination of the long-term population dynamics of *Harmonia* in Michigan suggests facilitation by the arrival of the soybean aphid. Coccinellid populations have been monitored annually since 1988 as part of a US National Science Foundation Long-Term Ecological Research (LTER) project at the Kellogg Biological Station. Yellow sticky card traps are deployed in crop and non-crop habitats on the station and monitored weekly throughout the growing
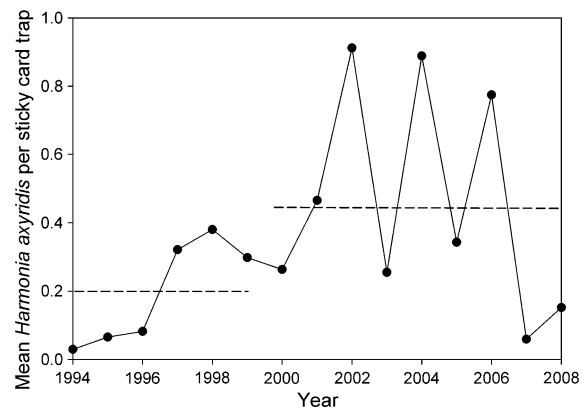
Fig. 3 Mean number of *Harmonia axyridis* captured on yellow sticky card traps placed in multiple crop and non-crop habitats at the Kellogg Biological Station Long-Term Research Site in Hickory Corners Michigan, 1994–2008. Dotted lines show the mean numbers of *H. axyridis* from 1994 to 1999 (before SBA) and from 2000 to 2008 (after SBA). Note the response of *H. axyridis* following years of local *A. glycines* outbreaks (2001, 2003, 2005)

season. The first report of *Harmonia* in Michigan in 1994 was detected as part of this sampling regime (Colunga-Garcia and Gage 1998). Over the first 6 years (1994–1999) of its occurrence at the Kellogg-LTER, *Harmonia* populations generally remained low, averaging 0.2 beetles per trap per week (Fig. 3). The soybean aphid was detected at the Kellogg-LTER in August 2000 and has been present at the site in every year since. Following the arrival of the soybean aphid, *Harmonia* populations more than doubled. Soybean aphid populations were generally low in 2000, 2002, 2004, and 2006–2008 but commonly exceeded economic injury levels in nearby commercial fields in 2001, 2003, and 2005. In outbreak years, soybean fields commonly averaged hundreds to thousands of aphids per plant in July and August. This new food resource was readily used by *Harmonia*. Adults responded by laying eggs in soybean and the resulting larvae had a nearly unlimited food source. As a result, particularly large flights of adult beetles were noted in the fall of aphid outbreak years. While this late season population increase was largely missed by the LTER coccinellid sampling that ended in August, the subsequent years' *Harmonia* counts were elevated (Fig. 3).

This pattern also suggests a mechanism for the apparent cyclical nature of the soybean aphid and *Harmonia* populations (Rhainds et al. 2010). The large numbers of *Harmonia* emerging in the spring

following outbreak years contribute to steady predation pressure on *A. glycines* populations. This keeps the soybean aphid population at relatively low levels and can prevent outbreaks from occurring (Costamagna and Landis 2006; Costamagna et al. 2007, 2008; Donaldson et al. 2007). However, it also has the effect of denying the subsequent generation of *Harmonia* the vast food resource that the outbreaks represent. Thus, fewer late season adults are produced and overwintering populations are smaller. This can lead to reduced *Harmonia* populations the following spring, less early season suppression of soybean aphid, and possibly mid-late season outbreaks. Detailed models have suggested a similar relationship for wheat aphids and coccinellid predators in Europe (Bianchi and van der Werf 2004). Other factors besides *Harmonia* also undoubtedly impact these cycles, including pathogens and unfavorable temperatures for aphid reproduction. Additional studies are required to better understand the relative roles of these factors in soybean aphid cycles.

In conclusion, several lines of evidence suggest that the arrival of soybean aphid has favored populations of *Harmonia*. It in turn has affected both native and introduced species, including direct and indirect impacts on humans.

Agonum muelleri. The carabid *A. muelleri* is native to Europe and was introduced into Newfoundland, Canada, in the 1840s (Hajek et al. 2007). The species reached New York state in the US by 1921, and has been recovered in various agroecosystems in the Northeastern US and Southeastern Canada since then (e.g. Shelton et al. 1983; Fan et al. 1993; Levesque and Levesque 1994; Byers et al. 2000; Belaoussoff et al. 2003; Cardenas and Buddle 2007; Shearin et al. 2007). In pitfall trapping studies done in soybean fields in New York State in 2004 and 2005, Hajek et al. (2007) found this species to be the most abundant of 60 species of ground beetles identified. Laboratory feeding studies also showed that *A. muelleri* readily fed upon soybean aphids and also that they climbed soybean plants in order to feed on them (Hajek et al. 2007; Hannam et al. 2008). In contrast to the situation in eastern North America, *A. muelleri* has been reported only very rarely in the North-Central US and adjacent parts of Canada (Bousquet and Larochelle 1993; Pearce et al. 2002) and not at all from soybean fields (Rutledge et al.

2004; M Gardiner and DA Landis unpublished; J Lundgren unpublished).

We briefly discuss two implications of these findings. First, Hajek et al.'s (2007) results suggest that the presence of soybean aphid may be contributing to an increase in abundance of an introduced species that had been present at relatively low densities for over 150 years. Whether or not this increase in abundance of *A. muelleri* will lead to negative impacts on native species has not been investigated, as far as we are aware. The second implication involves effects of high abundances of *A. muelleri* on soybean aphid densities. Hajek et al.'s (2007) studies revealed a negative correlation between trap catches of *A. muelleri* and soybean aphid densities, suggesting that this carabid may contribute to soybean aphid suppression in New York state. It seems likely that this species will eventually move into soybean fields in the North-Central US, in which case it could presumably contribute to biological control of soybean aphid in this region.

Aphelinus certus. *A. certus* is an Asian parasitoid found on soybean aphid in China, Korea, and Japan (Heraty et al. 2007). It has a broad host range, parasitizing aphids in at least four genera across two subfamilies of aphids and on at least four host plant species (KRH, unpublished data). *A. certus* has been found over a wide geographic range in the eastern US and Canada since 2005, thus it is likely that it was introduced either with the original introduction of soybean aphid or soon thereafter. Because of this broad host range, *A. certus* is very likely to parasitize aphids native to North America such as *Aphis oestlundi* and *Aphis monardae* which are closely related to soybean aphid (Desneux et al. 2009b).

Implications for management

Managing the harmful impacts of many of the pest species discussed above will best be accomplished by recognizing the chain of invasion events that may have led to their increases in abundance. In this section, we discuss potential implications for management that are attributable to the invasion meltdown scenario. In particular, we focus on two questions. First, does invasion meltdown imply that the reduction of particular facilitator species could benefit the management of facilitated invasive

species? Second, do meltdown dynamics affect other management options? Here, we will focus on classical biological control of soybean aphid, and the possibility that interactions with other invasive species may impact the effectiveness of this management strategy.

Implications of managing facilitator species

By definition, the removal of a species that facilitates other species should have detrimental effects on the facilitated species. Facilitator species are at the core of the invasional meltdown concept, and it follows that effective management of facilitator species within an invasional meltdown has the potential to reduce the abundance of species that benefit from the facilitator species. Taking advantage of such facilitative arrangements has been suggested for other invasional meltdown scenarios, including honeybees and scotch broom in Australia (Simpson et al. 2005) and a shrub and a tree species in Argentina (Tecco et al. 2007). In this latter case, the invasive shrub *Pyracantha angustifolia* acts as a nurse plant for seedlings of the invasive tree *Ligustrum lucida*, greatly improving sapling survival. Tecco et al. suggested that suppression of *P. angustifolia* should aid in efforts to control *L. lucida*.

Buckthorn as a facilitator species

Madritch and Lindroth (2009) have already shown that removal of *R. cathartica* might lead to reductions in abundance of exotic earthworms, and they alluded to the possibility that soybean aphid abundance could be reduced as a corollary benefit. We agree that this is a strong possibility and would add that the abundance of other invasive species could be reduced as well, including oat crown rust and flatworms that prey on earthworms (Fig. 1). Furthermore, to the extent that soybean aphid is a facilitator of *Harmonia* and other introduced consumers of the soybean aphid, reducing buckthorn abundance may indirectly limit the abundance of these species.

The key question concerning buckthorn removal is how feasible effective removal is at a broad geographical scale. Well-established populations of *R. cathartica* can have stem densities of several thousand per ha, cut stumps resprout unless chemically treated, and the seedbank remains viable for

5 years after adults are removed (Converse 1984; Pergams and Norton 2006; Delanoy and Archibold 2007). Individual stems can be treated with oil-based glyphosate or triclopyr applications (which can be done during winter), or stems can be cut and the herbicide applied to the cut stump during the growing season (Reinartz 1997; Converse 1984). Buckthorn can also be top killed by burning. However, stumps will continue to sprout and repeated burning annually for several years is necessary to kill European buckthorn (Huebner 2006; Bowles et al. 2007). Monitoring of uninfested areas and early removal of germinants by pulling is an effective way to keep European buckthorn from invading new areas, but it requires constant vigilance (Converse 1984). Managing the forest for dominance by late-successional species such as sugar maple, rather than oaks, may reduce the abundance of *R. cathartica* regeneration, because maple forests cast denser shade (Knight et al. 2007). Reduction of *R. cathartica* on a large scale would clearly require a lot of work, take several decades to complete, and be an expensive undertaking.

The extent to which local eradication or reduction of buckthorn near soybean fields would limit local colonization of soybean aphids is unclear and a promising area of future research as we have noted above. The occurrence of *Rhamnus* spp. near agricultural zones in Asia is highly restricted (GE Heimpel, KR Hopper, K Hoelmer, K Wu unpublished), and this may be in part because farmers are aware of the role of these shrubs as overwintering hosts for soybean aphids and strive to eliminate them from the vicinity of their fields (communicated by local agriculture officials to K. Hoelmer during foreign exploration for soybean aphid parasitoids in northeastern China). Biological control of *R. cathartica* in North America is currently under investigation (Gassmann et al. 2008), but no releases are planned in the near future.

The spores of oat crown rust disperse long distances, and a regional approach would likely be needed to control this pathogen by buckthorn management. A cautionary tale along these lines involves wheat stem rust, *Puccinia graminis*, which has a life cycle similar to oat crown rust. Wheat stem rust aeciospores overwinter on various species of barberry, *Berberis* spp., and a massive barberry eradication program was undertaken in the 1920s with the goal of suppressing wheat stem rust. While eradication of barberry was largely successful in the North-

Central US, windborne cereal stem rust uredospores dispersed from the South (where the rust can overwinter on cereals) and these dispersal events occurred early enough to cause major epidemics of wheat stem rust in the upper midwest. Thus, eradication of the overwintering host was deemed largely ineffective as a means of wheat stem rust control (Roelfs 1989).

In summary, region-wide eradication, or at least substantial reduction in abundance of, *R. cathartica* would likely be needed to improve management of oat crown rust, and even then there is a possibility of alternative overwintering modes. The relationship between soybean aphid and *R. cathartica* may be more obligate than this in the North-Central US but eradication may still be needed on a regional scale given the mobility of the aphid (Zhang et al. 2008; Michel et al. 2009). Buckthorn removal is a difficult undertaking and has not been achieved on a large scale in North America. To the extent, however, that controlling *R. cathartica* could lead to reductions in abundance of multiple invaders that are major environmental and/or economic pests, (e.g. European earthworms, oat crown rust, soybean aphids and *Harmonia*), it is conceivable that the resources of multiple stakeholder groups could be combined to improve the scope of control efforts.

Soybean aphid as a facilitator species

To the extent that soybean aphid abundance drives the abundance of its consumers, effective management of soybean aphid should lead to reduced abundance of these consumers. A number of both native and introduced predators, parasitoids and pathogens have been documented consuming the soybean aphid since its introduction in North America in 2000 (e.g. Rutledge et al. 2004; Nielsen and Hajek 2005; Mignault et al. 2006; Kaiser et al. 2007; Chacon et al. 2008; Noma and Brewer 2008) and the presence of soybean aphid could lead to enrichment of any of these species. Such enrichment could lead to a number of indirect ecological effects, chief among these being apparent competition, where an increase in abundance of a consumer of one species leads to increased consumption of one or more different species (Holt and Lawton 1994).

We focus here on the possibility that soybean aphid is leading to enrichment (increased abundance)

of *Harmonia*, as it is often cited as the most abundant and important exotic consumer of the soybean aphid in North America (Fox et al. 2004; Rutledge et al. 2004; Costamagna et al. 2007; Mignault et al. 2006; Donaldson et al. 2007; Chacon et al. 2008; Gardiner et al. 2009a, b). If elevated soybean aphid densities lead to *Harmonia* enrichment, effective soybean aphid management strategies should lead to reduction in *Harmonia* abundance.

Soybean aphid management is currently achieved by insecticide use. The most commonly-used insecticides are the pyrethroid λ-cyhalothrin and the organophosphate chlorpyrifos, which both provide consistent and effective control (Myers et al. 2005; Ragsdale et al. 2007) and to a lesser extent the neonicotinoid seed treatment thiamethoxam, which provides less consistent control (Magalhaes et al. 2009). These first two insecticides have a very broad spectrum of toxicity, and so likely kill *Harmonia* in addition to soybean aphids when both insects are present in soybean fields during applications. Field studies indicate that *Harmonia* aggregate to areas of high soybean aphid density (Fox et al. 2004; Donaldson et al. 2007; Chacon and Heimpel in press) so this dual-management effect could be fortuitous at relatively high aphid densities from the standpoint of managing *Harmonia* as a pest. The economic threshold for soybean aphid is currently set at 273 aphids per plant (Ragsdale et al. 2007), which is a density sufficient to attract *Harmonia* in small-plot outbreak situations (Fox et al. 2004; Donaldson et al. 2007).

Biological control introductions using Asian parasitoids are being attempted against the soybean aphid, but it is not yet clear whether they will be effective (Heimpel et al. 2004b; Wyckhuys et al. 2007a; Chacon et al. 2008). *Harmonia* aggregation and reproduction could in principle be reduced if biological control could maintain soybean aphid at densities low enough to either discourage colonization or oviposition, or reduce fitness if colonization and/or reproduction did occur. Biological control could produce a dual benefit in this case by controlling both soybean aphid (directly through parasitism) and *Harmonia* (indirectly through competition). Competition is rarely used or recognized as a mechanism for achieving biological control of arthropod pests, but it can be effective (Moon 1980; Hougen-Eitzman and Karban 1995; Nichols et al. 2008). As we discuss below, the competitive interactions between soybean aphid parasitoids and

Harmonia are complicated by the fact that *Harmonia* feeds on parasitized soybean aphids, but this dynamic need not exclude exploitative competition of the kind that would have negative impacts on *Harmonia*.

Biological control introductions within an invasional meltdown

To date, two Eurasian parasitoid species have been released against the soybean aphid in North America—*Aphelinus atriplicis* (referred to previously as *A. albipodus*; Wu et al. 2004b; Heraty et al. 2007), which was introduced into N. America against the Russian wheat aphid in the early 1990s (Hopper et al. 1998; Heraty et al. 2007) and also released against the soybean aphid in 2002 (Heimpel et al. 2004a), and *Binodoxys communis* (Wyckhuys et al. 2007a, b, 2008a, b, 2009; Desneux et al. 2009a, b), which was intentionally introduced beginning in 2007. Several other species are under investigation (Desneux et al. 2009c; Stary et al. 2010; KR Hopper, unpublished data). Here, we ask whether any of the facilitations discussed here are likely to affect the efficacy or safety of these biological control efforts. In particular, we focus on the possible roles of: (1) *Harmonia* in interfering with soybean aphid biological control in light of the fact that it is likely facilitated by soybean aphid itself, and (2) European buckthorn in affecting the overwintering ecology of Eurasian parasitoids imported against the soybean aphid.

### Harmonia and soybean aphid biological control

Paradoxically, while effective biological control could help manage *Harmonia* as we have discussed above, *Harmonia* itself may prevent biological control from being effective. *Harmonia* larvae and adults readily feed on parasitized aphids in the field, including mummified soybean aphids (Chacon et al. 2008; Chacon and Heimpel in press; Costamagna et al. 2008). Our observations in China suggest that abundances of *Harmonia* and other coccinellids are relatively low (as is the density of soybean aphids), resulting in a relatively low rate of predation on mummies (Table 1). In North America, however, densities of both soybean aphids and *Harmonia* can be orders of magnitude higher, and we have observed very high rates of mummy predation under these circumstances (Fig. 4). These observations are

Table 1 Summary statistics describing the per-plant densities of soybean aphids (all stages combined), *Binodoxys communis* mummies, and chewing predators (coccinellid larvae and adults) from 40 plants sampled on August 10 and 12, 2005 in an unsprayed soybean field within an agricultural experiment station in Lang Fang, China

Parameter	Mean ± SEM or proportion (*n*)
Mean number of soybean aphids	15.6 ± 2.1
Mean number of *B. communis* mummies	1.8 ± 0.3
Mean number of chewing predators*	0.05 ± 0.04
Proportion mummies chewed**	0.10 (850)

* Coccinellidae; larvae and adults with egg masses counted as 1

** From a larger sample of mummies sampled at the same site and dates but different plants
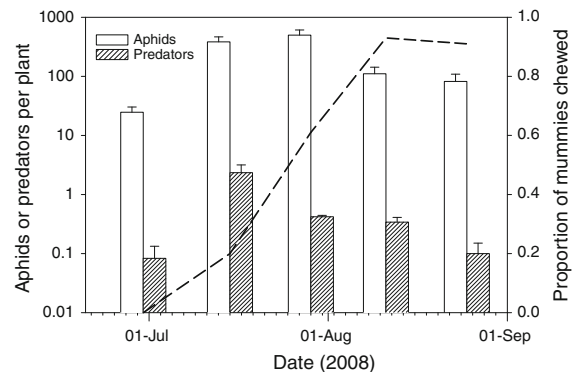
Fig. 4 Soybean aphid and aphid predator densities, along with the proportion of soybean aphid parasitoid mummies chewed by predators following a release of *B. communis* in St. Paul, MN, USA in summer 2008. Aphid and predator densities are means ± SEM (*n* = 8 release sites within one field). Over 75% of the adult predators were *Harmonia axyridis*, and the numbers of parasitoids represented in the proportions were 9, 393, 390, 255 and 108 pooled over the 8 sites) for each of the 5 sampling dates in chronological order

consistent with the hypothesis that predation of soybean aphid parasitoid mummies by *Harmonia* is higher in North America than it is in China. Previous studies report aggregation of *Harmonia* to high densities of soybean aphid (Fox et al. 2004; Donaldson et al. 2007), and Chacon and Heimpel (in press) have shown that predation on mummies by chewing predators such as *Harmonia* increases with soybean aphid density. It is therefore likely that the high abundances of soybean aphid found in North America favor intraguild predation of parasitoids by aphid

predators (in particular *Harmonia*), endangering successful biological control in areas with high soybean aphid and *Harmonia* abundances. This suggests the hypothesis that establishment of parasitoids may be best achieved at low soybean aphid densities.

Buckthorn and soybean aphid biological control

Diapause in aphid parasitoids typically occurs within the host, and may be influenced by photoperiod, temperature, host stage attacked, and plant quality (Polgár and Hardie 2000). Given the tight linkage between overwintering soybean aphids and European buckthorn in North America, a fundamental question emerges: do Eurasian parasitoids released against soybean aphid follow their host to buckthorn to overwinter? The relative paucity of *Rhamnus* in the native range of the soybean aphid may favor the use of alternative aphid hosts by soybean aphid parasitoids during the overwintering period. Alternatively, parasitoid traits facilitating the location of, and/or migration to, buckthorn may exist that permit high fidelity between soybean aphid and its parasitoids in the fall months. A deeper understanding of the overwintering biology of these biological control agents is essential, as reliance on alternative aphid hosts for diapause could either decrease the likelihood of parasitoid establishment (if introduced or native North American aphid species cannot substitute for Asian alternative hosts) or increase their environmental risks (if native North American aphid species are used as overwintering hosts).

An active research effort is ongoing with respect to the overwintering biology of *B. communis* (MK Asplen and GE Heimpel unpublished). Laboratory studies demonstrate that *B. communis* can successfully complete development on both soybean aphid gynoparae (fall female migrants from soybean to buckthorn) and oviparae, but not in adult male aphids. Furthermore, *B. communis* successfully reproduced after release into field caged *R. cathartica* bushes seeded with lab-produced soybean aphid gynoparae. In both the laboratory and the field studies, mummification rates of oviparae appear much higher than those of gynoparae. Together, these observations suggests that *B. communis* may be capable of utilizing soybean aphid on *R. cathartica* in

the North-Central US, although successful overwintering by *B. communis* has not been verified following any North American release.

If Eurasian soybean aphid parasitoids use buckthorn as their primary overwintering hosts, then migration from soybean to buckthorn would be an essential component of their life histories. Two avenues of movement may be open to migrating parasitoids: (1) direct flight by adult parasitoids, or (2) passive transport as eggs or early instar larvae inside alate aphids (Rauwald and Ives 2001, Feng et al. 2007). The latter has been hypothesized for *B. communis* based on the early timing of spring soybean colonization in China (Hoelmer and Kirk 2005), and the findings of both successful parasitism of alatoids and alate soybean aphids coupled with a significant developmental delay (Wyckhuys et al. 2008a, b). In a more direct examination, studies of alate soybean aphid flight performance following parasitism by *Aphelinus varipes* showed similar flight performance between unparasitized aphids and both aphids parasitized as alates and alatoids parasitized with 24–48 h of flight (Zhang et al. 2009). A more complete understanding of the patterns and frequency of alate-assisted parasitoid movement is currently needed to assess its impact on soybean aphid biological control introductions. It is possible, for example, that transport of parasitoids within alates would facilitate establishment during fall migrations (when their potential overwintering hosts are moving to buckthorn), but hinder it during summer migrations (due to population spreading and resulting issues with transported parasitoids finding mates [the Allee effect]). Furthermore, the relative frequency of alate-assisted movement may be important in determining how well introduced parasitoids follow their target host populations, which may be an important factor in successful biological control (Zhang et al. 2009). Finally, *Harmonia* predation on parasitized aphids on buckthorn may represent another avenue by which this predator may interfere with parasitoid-based biological control.

Conclusions

One of our goals in writing this paper was to assess the hypothesis that all or some of the species depicted

in Fig. 1 are involved in a multi-species invasional meltdown. Simberloff (2006) envisioned a community-level phenomenon in which various forms of interspecific facilitation among exotic species lead to 'an increasing rate of establishment of introduced species/and or an accelerating impact'. Our web of interactions suggests just such a scenario: mutual facilitation between European earthworms and buckthorn increased the spread and impact of both of these species, with European starlings possibly aiding in the spread of buckthorn as well. Without the widespread presence of European buckthorn, it seems unlikely that either oat crown rust or soybean aphid would have established in North America, despite the previous introduction of their summer hosts—oats and soybeans. Soybean aphid has spread spectacularly in North America in less than a decade and now commonly becomes very abundant in a crop that had previously harbored no aphids. Such a sudden increase in a highly nutritious food source is expected to lead to population-level enrichment of aphid consumers. One of these enriched consumers appears to be *H. axyridis*, an important invasive species in its own right. As we stress in the body of this paper, some of these links are circumstantial and some of the data is fragmentary. A large part of our motivation for writing this article, however, was to articulate specific hypotheses and spur research that would test the more general hypothesis of invasional meltdown in this and other systems.

Invasion meltdown dynamics (or facilitation more generally) should have important implications for the management of invasive species. In particular, successful management of a facilitator species should lead to decreased abundance of the species that are facilitated. Targeted earthworm reduction does not seem promising along these lines because there is no known way to remove invasive earthworms. Even if such efforts were successful, existing buckthorn would persist for several decades. It is conceivable that the *Bipalium adventitium* invasion may eventually partially accomplish this goal, but research in this area is lacking. Intervention into the meltdown sequence would likely be more effective at other levels. Buckthorn reduction, in particular, would have the advantage of impacting multiple secondary invaders including soybean aphid, oat rust and *H. axyridis* and it could prove to be the most cost-effective means of reducing multiple ecosystem disservices. Due to its status as an invader of natural ecosystems, coalitions of environmental and agricultural interests may align to cooperate in a regional effort. Creative synergies may also exist in the generation of alternative energy. For example, buckthorn biomass that is removed as part of restoration efforts may be burned for energy production in co-firing electrical plants (B. Spears, personal communication).

Invasional meltdowns may have particular implications for biological control, and we consider this possibility for biological control introductions against the soybean aphid using parasitoids. One likely effect involves *H. axyridis*, which appears uniquely favored by soybean aphid infestations. This lady beetle feeds on parasitized as well as unparasitized aphids and its enrichment in areas of aphid outbreak may limit the ability of parasitoids to establish or have strong effects on soybean aphids. The strong link between soybean aphids and *R. cathartica* also poses potential challenges for biological control if parasitoids are not able to use soybeans or if they are attacked there by *Harmonia*.

In conclusion, some of the interactions that we explore in this paper are demonstrably facilitative and may collectively constitute an extensive invasional meltdown. Further research in this and similar systems should be aimed at testing the hypothesis that meltdown dynamics are occurring and also the hypothesis that invasive species management could be improved by considering particular implications of facilitative interactions.

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