

COMMENTARY

Invasive species, disrupted chemical community dynamics and future adaptations: Commentary on Chabaane *et al.* 2015

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Chabaane *et al.* (2015) describe the subtle disruptive chemical changes that an alien herbivore (a moth caterpillar, *Spodoptera littoralis*) may cause in a native community. This disruption is described across trophic links from the plant it eats (a mustard family species, *Brassica rapa*) to native herbivores (the cabbage white butterfly, *Pieris brassicae*) and their native natural enemies (parasitic wasps, *Cotesia glomerata*). This paper reinforces the concern that new insect species arriving in natural communities may potentially have a detrimental impact: inducing unexpected changes in plant chemistry; altering competitive interactions with other herbivores; and changing the dynamics of the natural enemies of such herbivores. Extreme disruptions by 'invasive' Lepidoptera include pest population outbreaks that may cause large-scale defoliations which affect the entire ecosystem by cascading chemical, physiological and ecological changes across all trophic levels. In consequence altering the functional dynamics in various ways (Redman & Scriber 2000; Kenis *et al.* 2009; Gandhi & Herms 2010). The study by Chabaane *et al.* (2015) shows how subtle changes in chemical cues from alien herbivores may result in major changes with cascading responses of the native plant–herbivore–parasite community.

Whether such chemically based disruptions such as those described by Chabaane *et al.* (2015) result in local population outbreaks, and whether such changes become part of the future community dynamics, depends on the intensity and variability of natural selection that occurs. All of these biotic interactions resulting from invasive species are shaped by a combination of ecological and evolutionary processes (Moran & Alexander 2014). The fundamental component at all levels (organism, population, community and ecosystem) is the underlying genetic variability, which both interacts with and shapes all aspects of the phenotypes (phytochemical, biochemical, behavioural, physiological and morphological traits) and the potential for rapid adaptation and introgressive gene flow (Brasier 2001; Scriber 2011; Franks & Hoffmann 2012; Pauls *et al.* 2013). Plant genotypes can shape communities and drive evolutionary change ('community genetics'; Smith *et al.* 2011). Similarly, underlying genetics shape interactions and natural selection across different environmental gradients at the landscape and ecosystem levels ('geographic mosaic of

co-evolution'; Thompson 2005). Understanding the underlying chemical, ecological and genetic sources of evolutionary responses to invasive species in the face of rapid environmental changes (such as global warming) will become one of the most significant challenges in the next decade (Moran & Alexander 2014; Scriber 2014). There is clearly a need for additional studies such as Chabaane *et al.* (2015) because the impacts of introduced species may run contrary to expectation. Illustrated by the fact that the alien (potentially invasive) herbivore species caused disruptive impacts on the community via induced changes in plant chemistry. This occurred despite the fact that exotic herbivores themselves were not actually used as hosts by the native parasitoids.

Chabaane *et al.* (2015) show that exotic herbivores may invade new environments where they can significantly alter the native communities. This is done via both direct (induced changes in plant phytochemistry or nutritional ecology; Scriber 2002; Gandhi & Herms 2010) and indirect (cascading) impacts on species across trophic levels in the ecosystem (Redman & Scriber 2000; Dicke & Baldwin 2012; Stam *et al.* 2014). The chemical basis of these plant/herbivore/enemy interactions has historically focused on host plant resistance, herbivore counter-adaptations and chemical defenses derived from the plants or herbivores in a relatively recent field of chemical ecology (Price *et al.* 1980; Feeny 1992; Gols 2014). Changes in other abiotic factors (e.g. climate and local drought conditions, as well as stoichiometry; Mattson & Scriber 1987; Mattson & Haack 1987; Elser *et al.* 2000; Chuncu 2014) can also greatly alter the chemical ecology of the community, including interactions of plants, herbivores and their enemies (predators, parasites, and pathogens: Stamp 1993; Ayres & Lombardero 2000; Singer & Stireman 2005). However, Chabaane *et al.* (2015) show that changes in the chemical environment are not always ecologically predictable.

More ground-breaking research as described in the interactions of chemical components among native and exotics across local populations and trophic levels will be required in the future (Chabaane *et al.* 2015). However, the elucidation of the genetic basis of ecological ripples caused by allelochemical interactions will likely be the next major step in better understanding the autecological (organism & population) causes of synecological responses in the community and ecosystem (Whitham *et al.* 2003; Wheat *et al.* 2007; Stam *et al.*

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2014). It is important to remember that species-level analyses alone may miss much intraspecific and even interspecific variation, from genomic biochemistry to chemically detected predator or parasitoid interactions with prey. Ecological dangers of 'invasive species' have become widely recognized and increasingly common, perhaps due to the global nature of many ecological interactions resulting from human-induced transport. However, 'invasive genotypes' are less well recognized (or unrecognized), but may be no less important, especially with the increasingly revealed occurrences of animal hybrid speciation as well as plant hybrid speciation (Abbott *et al.* 2013; Scriber 2014). As additional 'biochemical waves' of community change are discovered and described for invasive species such as the *Spodoptera* (Chabaane *et al.* 2015), the underlying 'ripples of genetic change' evolving or co-evolving in such associated native communities also need to be assessed.

Interspecific hybrids in plants may significantly alter ecological patterns of allelochemical interactions in a community through variation in levels of resistance to herbivores (Strauss 1994) or degrees of susceptibility to parasites in animals (Fritz, Moullia & Newcombe 1999). Host plant chemistry may also differentially impact immune responses in insect herbivores (Lampert 2012). Such complexity in phenotypic and genotypic composition and function across trophic levels will be better understood only through a combination of additional studies of genetic as well as allelochemical variation (Stam *et al.* 2014). The impact of non-native invasive species, their chemical impacts and introgressive hybrid genotypes on native communities will certainly be of increasing importance during the next two decades (Rodriguez-Saona, Blaauw & Isaacs 2012; Moran & Alexander 2014). The genetic versus phenotypic bases (including plasticity) of these biochemical factors that mediate and control interactions should be part of these investigations.

Synthesis

Several decades ago phytochemistry integrated successfully with ecology. Now, the confluence of the genetic foundations of allelochemically mediated multiple-trophic-level interactions can be expected to surface and become the fundamental focus among researchers in the near future. Ground-breaking chemical analyses revealing unexpected ecological responses, such as Chabaane *et al.* (2015) describe, will be a fundamental necessity in assessing the relative contributions of genetic evolution, phenotypic flexibility and environmental variability in subsequent community dynamics. Adaptations to rapidly changing environmental conditions (e.g. global warming) will likely emerge in quickly evolving genotypes throughout the world's ecosystems. In fact, reshuffling species and genes through both ecological and introgressive genetic invasions may play a critical role in their ability to survive and adapt in communities of the future (Seehausen, Takimo & Jokela 2008; Chunco 2014; Scriber 2014). In the full light of 'chemical ecology' currently, the dawn of 'ecological genomics' is upon us, and the possibilities for success in our

management of natural and agro-ecosystems are enormously enhanced.

Data accessibility

This paper does not contain data.

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