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Novel chemicals engender myriad invasion mechanisms

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Tansley review

Novel chemicals engender myriad invasion mechanisms

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Summary

Non-native invasive species (NIS) release chemicals into the environment that are unique to the invaded communities, defined as novel chemicals. Novel chemicals impact competitors, soil microbial communities, mutualists, plant enemies, and soil nutrients differently than in the species' native range. Ecological functions of novel chemicals and differences in functions between the native and non-native ranges of NIS are of immense interest to ecologists. Novel chemicals can mediate different ecological, physiological, and evolutionary mechanisms underlying invasion hypotheses. Interactions amongst the NIS and resident species including competitors, soil microbes, and plant enemies, as well as abiotic factors in the invaded community are linked to novel chemicals. However, we poorly understand how these interactions might enhance NIS performance. New empirical data and analyses of how novel chemicals act in the invaded community will fill major gaps in our understanding of the chemistry of biological invasions. A novel chemical-invasion mechanism framework shows how novel chemicals engender invasion mechanisms beyond plant–plant or plant–microorganism interactions.

I. Introduction

Humans, intentionally or accidentally, introduce plants into non-native ranges. Some introduced species become abundant and spread to expand their ranges. These species are identified as non-

native invasive species (from this point forwards called NIS). As an NIS establishes in a new range, it may introduce chemicals previously absent from the recipient community, identified as novel chemicals (see Box 1). It is assumed that resident communities including soil microbes do not produce the chemicals

introduced by the NIS (Callaway & Ridenour, 2004). Differences in chemical function between native and non-native ranges can occur because long-standing evolved interactions involving chemistry in the native range can be disrupted in non-native ranges. Differences in phenotypic expression of the chemical functions of an NIS might occur across habitats within its native range (Ehlers *et al.*, 2020) or in the non-native range (Palacio-López & Gianoli, 2011). Because most NIS evolved in an environment different from that of the non-native range, the chemicals they produce can play distinctly different ecological and physiological roles there. Many hypotheses have been proposed to explain the invasion success of NIS, yet no single hypothesis can be considered to be more successful than others at explaining most invasions (Catford *et al.*, 2009; Gurevitch *et al.*, 2011; Lau & Schultheis, 2015). Novel chemicals can strongly influence soil microbial communities, competitors, plant enemies, and soil properties (Callaway *et al.*, 2008; Inderjit *et al.*, 2011b; Zheng *et al.*, 2015) and drive mechanisms that support invasion hypotheses, including the novel weapons hypothesis (NWH; Box 2) and the disruption of mutualistic associations (Box 2; Callaway & Ridenour, 2004; Inderjit *et al.*, 2011b; Inderjit, 2012; Zheng *et al.*, 2015). However, how novel chemicals affect soil feedbacks, fitness, plant enemies, (apparent) competition, and nutrient availability is still not well understood. In contrast with a strong theoretical basis (Enge *et al.*, 2013; Jogesh *et al.*, 2013; van der Putten *et al.*, 2013; Brouwer *et al.*, 2015), there is a dearth of experiments studying the role of novel chemicals in most invasion hypotheses. Allelopathy, as opposed to novel chemicals, is a term used generally to identify growth-inhibiting impacts on neighbouring plants via chemicals released by a focal plant species without consideration of the specific mechanism(s) generating the impact. Because the focus of this review is the potential role of novel chemicals in invasion hypotheses, we will not use the generic term 'allelopathy' but

instead focus on the functions of novel chemicals as they relate to NIS. Important unanswered questions are: What are the ecological functions of these novel chemicals? and What role(s) do novel chemicals play in mechanisms underpinning different invasion hypotheses?

The performance of many native plant species is, at least partly, determined by interactions with the soil microbial community, native plant chemistry, soil nutrients, mutualists, and natural enemies (van der Putten *et al.*, 2001; Inderjit *et al.*, 2011b; Austin *et al.*, 2014; Kos *et al.*, 2015; Bonanomi *et al.*, 2017; Kostenko *et al.*, 2017; Heinen *et al.*, 2019; Veen *et al.*, 2019; Huberty *et al.*, 2020; Pineda *et al.*, 2020). For example, beneficial soil microbes can reduce negative effects of aboveground insect herbivory on plant growth (Pineda *et al.*, 2017, 2020; Heinen *et al.*, 2019). Some NIS culture soil biota beneficial to themselves (Callaway *et al.*, 2004), but whether a beneficial soil biota cultured by an NIS will lower its herbivore damage is unknown. The composition of the soil microbial community in the rhizosphere of the NIS is influenced by the chemicals it releases. Changes in the soil microbiome can influence the performance of aboveground plant-feeding insects indirectly by changing the composition of plant chemicals (Heinen *et al.*, 2019) or directly by influencing the microbiome inside the insect herbivores (Hannula *et al.*, 2019). Despite recent evidence for such microbiome–plant–insect interactions (Hannula *et al.*, 2019; Pineda *et al.*, 2020), we poorly understand how changes in soil microbial communities mediated by NIS affect their chemistry and interactions with aboveground herbivores. Furthermore, these plant-mediated effects on the soil microbial community, in turn, can influence the performance or chemistry of other neighbouring plants and of plants that subsequently grow in the same soil. Linkages among novel chemicals, soil microbial communities, soil nutrients, mutualists, and plant enemies can all influence NIS performance and therefore influence invasiveness. Efforts to link hypotheses such as the NWH, evolution of increased competitive ability (EICA, Box 2), and defence against enemies (Blossey & Nötzold, 1995; Feng *et al.*, 2009; Zheng *et al.*, 2015) have been limited. Novel chemicals produced by NIS can support several invasion hypotheses that predict NIS invasion success (e.g. Kalisz *et al.*, 2014).

Our first goal is to discuss how novel chemicals affect almost all interactions an NIS may have with its surrounding biotic environment and how they can underpin different invasion hypotheses. Several frameworks have been discussed to highlight the importance of various invasion hypotheses (e.g. Catford *et al.*, 2009; Gurevitch *et al.*, 2011; Heger *et al.*, 2013). However, existing proposed invasion frameworks do not explicitly discuss how novel chemical-mediated effects of invaded range communities could lead to impacts envisioned by more than one invasion hypothesis, that is plant–soil feedbacks, production of novel chemicals, and NIS experiencing induced defence against generalists simultaneously. Our second goal is to develop a framework that clarifies linkages among novel chemistry, competitors, soil communities, mutualists, plant enemies, and nutrient cycling. Our proposed framework elucidates linkages involving novel chemicals at various levels of biological organisation and how they facilitate NIS invasion success. We need more comprehensive knowledge of how multiple invasion hypotheses can explain the invasion of a single

Box 1 Definition of novel chemicals.

Plants release many different chemicals into the environment that protect against enemies, affect neighbouring plant performance, alter the abundance and diversity of soil microbial communities, and mediate soil properties (Kessler & Baldwin, 2002; Weidenhamer & Callaway, 2010; Inderjit *et al.*, 2011b; Ehlers *et al.*, 2020). Processes including foliar leaching, root exudation, litter decomposition, and volatilisation deposit chemicals into the environment.

Some plants introduced far from their native range became abundant and invasive and are identified as NIS. Non-native invasive species may introduce unique chemicals not previously experienced by invaded communities (competitors, soil microbes, herbivores, pathogens) and produce them in significantly higher quantities than in the invaded community, therefore causing their ecological functioning to differ greatly from when they are released by a species in its home environment (see Callaway & Ridenour, 2004; Inderjit *et al.*, 2011b). Here we focus on these 'novel chemicals', defined as chemicals released by NIS that impart competitive or fitness advantages related to sensitive competitors, naïve soil microbes, or protection from enemies (see Box 2). Novel chemicals interact with biotic and abiotic ecosystem processes and factors and mediate invasion mechanisms.

Box 2 Glossary of invasion mechanisms linked to defence, novel chemicals, soil microbial communities, and resource fluctuations.

Novel weapons hypothesis (NWH): Non-native invasive species introduce chemicals into their non-native ranges that are novel for resident communities and therefore identified as novel chemicals. Novel chemicals may be interpreted in various ways for their novelty in non-native ranges as discussed in Fig. 2; Table 1. Non-native invasive species bring chemicals that are novel for the resident plant community and generate impacts largely because of the presence of sensitive resident communities and naïve soil microbial communities, as predicted by the 'novel weapons hypothesis' (Callaway & Ridenour, 2004). That is why the NWH has also been identified as 'allelopathic advantages against resident species' (AARS) (Callaway & Ridenour, 2004). The NWH is based on the venerable phenomenon of 'allelopathy' and predicts that chemicals released by a plant species into the environment can suppress growth of neighbouring species (Inderjit & Callaway, 2003).

Plant–soil feedbacks (PSFs): When plants induce changes in abiotic and biotic soil properties that subsequently affect growth of other plants of the same or different species, this is called 'plant–soil feedback' (van der Putten *et al.*, 2013). Most attention is paid to plant-induced changes in soil microbial communities, and this focus has resulted in an in-depth understanding of plant–soil microbial feedbacks (Callaway *et al.*, 2004; Inderjit & van der Putten, 2010). Novel chemicals have long been known to influence abundance, diversity, and functioning of soil microbes (Inderjit, 2005), yet we do not know whether novel chemicals play a role in mediating or altering PSFs. Recently, Veen *et al.* (2019) provided evidence for litter-mediated PSFs. Relatively little attention has been paid to plant-induced changes in abiotic soil properties and their possible impact on plant growth. Convincing evidence does exist for litterfall-mediated species-specific effects on soil chemistry, also known as the 'Zinke effect' (Zinke, 1962; Waring *et al.*, 2015). It will be important to study linkages between novel chemicals and plant-induced abiotic and biotic soil factors, because plant chemicals can influence both abiotic and biotic soil processes and properties directly and indirectly.

Evolution of increased competitive ability (EICA) and enemy release hypothesis (ERH): One hypothesis to explain the invasion success of non-native species in their introduced ranges is the 'enemy release hypothesis' (Keane & Crawley, 2002), which predicts that non-native species lack specialist enemies (herbivores and pathogens) at least early during an invasion. Absence of specialist enemies results in reallocating resources from costly defence against enemies to growth and/or production of less costly defence chemicals, as predicted by the 'evolution of increased competitive ability' hypothesis (Blossey & Nötzold, 1995). Reallocation of resources from defence to growth, particularly for shade-intolerant plants, is also known for other ecological processes such as 'shade avoidance responses' (Izaguirre *et al.*, 2006).

Shift-in-defence hypothesis (SDH): As a consequence of the ERH, resources are reallocated from the production of costly defence chemicals that are involved in reducing insect digestibility (e.g. proteinase inhibitors) to production of less costly defence chemicals (e.g. terpenes and glucosinolates) (Müller-Schärer *et al.*, 2004; Joshi & Vrieling, 2005; Doorduyn & Vrieling, 2011; Inderjit, 2012).

Fluctuating resource hypothesis (FRH): Soil nutrients play a critical role in shaping non-native plant invasions (Ehrenfeld, 2003; Weidenhamer & Callaway, 2010; Heckman *et al.*, 2017). Fluctuations in resource availability in the soil can result in competitive advantages to invasive species, as predicted by the 'fluctuating resource hypothesis' (Davis *et al.*, 2000; also see Li & Stevens, 2012).

NIS. The proposed novel framework aids visualising complex interactions in the invaded range communities and highlights the need to incorporate several invasion hypotheses in future studies. New experiments and analyses will be required to link novel chemicals, plant–soil feedbacks, competitive advantages to NIS against competitors, plant defence against enemies, mutualisms, and nutrient cycling in novel environments. Such studies would strengthen our understanding of the ecological role of novel chemicals in the fundamental processes that organise plant communities and drive ecosystem processes and fill a major gap in our understanding of how novel chemicals mediate diverse ecological processes and factors to facilitate plant invasion.

II. Novel chemicals introduced by NIS

Some NIS introduce chemicals in their non-native ranges that are considered 'novel' because they are released by a plant species not present previously and it is assumed that native plant species do not produce the same chemical. Most NIS in North America have been shown to possess potent novel chemistry lacking in native plant species (Cappuccino & Arnason, 2006). Novel chemicals provide competitive advantages to the NIS against native residents, suppress mutualists (e.g. mycorrhizal fungi) in non-native ranges but not in native ranges, and provide a low-cost defence against herbivorous enemies (Callaway *et al.*, 2008; Zheng *et al.*, 2015). Competitive advantages for an NIS against native species could be due to the presence of sensitive native species and naïve soil

microbial communities that cannot degrade novel chemicals, at least in the early stages of invasion (Callaway & Ridenour, 2004; Inderjit *et al.*, 2011b; Macel *et al.*, 2014). An NIS that produces more metabolites than native species is therefore more chemically distinct from them and is defended better against generalist herbivores (Macel *et al.*, 2014). Below we discuss different scenarios to show that biogeographic (native vs non-native ranges) variation exists in chemical production by plant species and to illustrate how novel chemicals function in the non-native ranges as envisioned by the NWH or to refine the hypothesis.

Non-native invasive species are known to produce novel chemicals not previously experienced by the recipient communities. Several examples show how novel chemicals provide such competitive and defensive advantages in non-native ranges (Table 1; Fig. 1). The forb *Chromolaena odorata* (Asteraceae, Siam weed) is native to the Americas and Caribbean and invasive in various habitats including forests, wastelands, and agricultural fields in Old World tropics and subtropics (Fig. 1a). Zheng *et al.* (2015) found that *C. odorata* produces more odoratin (a chalcone) in the non-native range than in its native range (Fig. 2a) and rhizosphere soil of *C. odorata* strongly inhibits germination and seedling growth of species native to China (non-native range) more than those from Mexico (native range). These authors also found that *C. odorata* has a poor defence against aboveground herbivores but can defend itself against soilborne enemies. In another study, Li *et al.* (2020) found that invasive populations of *C. odorata* produced greater quantities of

Table 1 Novel chemicals from some of the major non-native invasive species (NIS) that provide defence and competitive advantage to the invader in the non-native range.

Non-native invasive species	Novel chemicals	Ecological roles/impact on neighbours/soil microbes/plant enemies
<i>Ageratina adenophora</i> (native to Mexico; invasive in Asia)	2-Carene, α -phellandrene, β -pinene, bicyclogermacrene (<i>E</i>)- β -caryophyllene, and (<i>E</i>)- α -bergamotene	Biogeographical ^a variation in the production of terpenes; results support novel weapons hypothesis and role of volatiles in defence against enemies is argued (Inderjit <i>et al.</i> , 2011a)
<i>Alliaria petiolata</i> (native to Europe; invasive in North America)	Glucosinolates (sinigrin)	Sinigrin suppresses mycorrhiza, therefore disrupting their mutualistic associations with native plants (Lankau <i>et al.</i> , 2009; Lankau, 2012) Glucosinolates are reported to repel ungulates, therefore providing competitive advantages over native species (Kalisz <i>et al.</i> , 2014)
<i>Bonnemaisonia hamifera</i> (red alga; native to Japan; invasive in Scandinavia)	Apigenin flavonoids, alliarinoside, and isovitexin glucoside	Defence against herbivores (Haribal & Renwick, 2001; Haribal <i>et al.</i> , 2001)
<i>Calluna vulgaris</i> (native to North America; invasive in New Zealand)	1,1,3,3-Tetrabromo-2-heptanone	Greater defence against naïve native generalists (Enge <i>et al.</i> , 2012); competitive advantages over native macroalgae (Svensson <i>et al.</i> , 2013); refuge-mediated apparent competition (Enge <i>et al.</i> , 2013)
<i>Chromolaena odorata</i> (native to New World that is, America; invasive in Old World tropics and subtropics)	Mono-, homo- and sesquiterpenes	Biogeographic variation in the production of terpenes across invaded sites is attributed largely to variation in soil nutrients (Effah <i>et al.</i> , 2020)
	Odoratin	Higher amounts of odoratin in non-native ranges provide greater competitive advantages (Zheng <i>et al.</i> , 2015)
	Acutellerin-4',6,7-trimethyl ether, 4',5,6,7-tetramethoxyflavone, isosakuranetin, 3,5-dihydroxy-7,4'-dimethoxyflavone, dihydrokaempferol-3-methoxy ether, and kaempferide-4'-methoxy ether	Greater amounts of flavonoids in the non-native range provide competitive advantages and better defence against soilborne pathogens (Li <i>et al.</i> , 2020)
	Root leachates	Root leachates of <i>C. odorata</i> can drive accumulation of native soil pathogens (Mangla <i>et al.</i> , 2008)
<i>Centaurea diffusa</i> (native to Europe; invasive in North America)	8-Hydroxyquinoline	Facilitates uptake of soil iron, therefore providing competitive advantages over resident communities (Tharayil <i>et al.</i> , 2009)
<i>Datura stramonium</i> (native to Mexico; invasive in Spain)	Atropine and scopolamine	Greater amounts of two compounds in native range than in non-native range due to presence of specialist herbivores (Castillo <i>et al.</i> , 2019)
<i>Echium plantagineum</i> (native to Europe and Asia; invasive in Australia)	Naphthoquinones and pyrrolizidine alkaloids	Defend against insect and livestock herbivory and provide competitive advantages against weeds (Skoneczny <i>et al.</i> , 2019)
<i>Impatiens glandulifera</i> (native to Western Himalaya; invasive in Europe)	2-Methoxy-1,4-naphthoquinone (2-MNQ) 2-MNQ glycoside	Aqueous leaf and root extracts inhibit germination of native herbs and mycelium growth of ectomycorrhizal fungi (Ruckli <i>et al.</i> , 2014) Resistance of invasive populations to a generalist herbivore is linked to this chemical; no competitive advantage for the invader was observed against neighbour <i>Urtica dioica</i> (Gruntman <i>et al.</i> , 2017)
<i>Prosopis juliflora</i> (native to South America; invasive in arid and semiarid parts of Asia, Middle East, Africa, USA and Australia)	L-Tryptophan	Greater amounts of L-Tryptophan in invasive populations of <i>P. juliflora</i> than in native congeneric species <i>P. cineraria</i> (Kaur <i>et al.</i> , 2012)
<i>Rhododendron ponticum</i> (native to Iberian Peninsula, invasive in Britain and Ireland)	Nectar contains grayanotoxin I and III	Chemicals deter solitary mining honeybee and native honeybee but not common bumblebee species; floral nectar of the invader is found for those pollinators that can tolerate chemicals from <i>R. ponticum</i> (Tiedeken <i>et al.</i> , 2016)
<i>Senecio jacobaea</i> (native to Northern Eurasia; invasive in North America, Australia, and New Zealand)	Pyrrolizidine alkaloids	Greater production of alkaloids in non-native range than in native range; defence against generalists (Joshi & Vrieling, 2005)
<i>Solidago altissima</i> (native to USA; invasive in Europe and Japan)	Polyacetylenes for example dehydromatricaria ester (DME)	Greater production of polyacetylenes in invasive population (Japan) than native (USA) populations; DME inhibits neighbouring species (Uesugi & Kessler, 2016)
<i>Triadica sebifera</i> (native to China; invasive in North America)	Root exudates contain quercetin	Root exudates facilitate greater mycorrhizal colonisation of <i>T. sebifera</i> in the non-native range than in the native range (Tian <i>et al.</i> , 2021)

^aNative vs non-native ranges.

phenolic compounds; some of these phenolic compounds confer stronger defence and others may suppress native species (Table 1). Recently, Tian *et al.* (2021) recorded more quercetin, a flavonoid, in root exudates of 60-d-old or 90-d-old *Triadica*

sebifera plants from the non-native (USA) than from the native (China) range. Quercetin causes higher colonisation by arbuscular mycorrhizal fungi (AMF) of invasive populations of *T. sebifera* than of its native populations (Fig. 2b).



Fig. 1 Non-native invasive species that produce novel chemicals. (a) *Chromolaena odorata*, (b) *Ageratina adenophora*, (c) *Alliaria petiolata*, and (d) *Prosopis juliflora*. Details of novel chemicals that provide defence against enemies or neighbours of the non-native species are given in Table 1. Photographs by Susan Kalisz (c) and Inderjit (a, b and d).

By contrast, lower production of costly chemicals in non-native ranges than in the native range is likely related to the absence of specialist enemies. For example, production of two tropane alkaloids, atropine (Fig. 2c, upper panel) and scopolamine (Fig. 2c, lower panel), was 40 and 20 times greater, respectively, in Mexico, the native range of *Datura stramonium* (Solanaceae, jimson weed), than in Spain, its non-native range (Castillo *et al.*, 2019). The greater production of these two chemicals in the native range was related to the presence of specialist enemies (Castillo *et al.*, 2019; Table 1). Therefore, NIS may produce greater quantities of novel chemicals involved in competition with other plants, but production of chemicals that defend against specialist enemies may decline in their non-native ranges. If such defences are inducible, NIS may not produce costly chemicals needed to defend against specialist enemies (herbivores and or pathogens) when these are absent in the non-native range. In such cases, energy (resources) may be reallocated to other functions including production of low-cost novel chemicals that provide competitive advantages to NIS against generalist enemies in its new community, as predicted by EICA.

Non-native invasive species produce a suite of chemicals in their native ranges. Several studies have shown biogeographic variation in novel chemical production, where production of certain chemicals is higher but that of others may be lower in the non-native range of the NIS than in its native range. For example, Inderjit *et al.* (2011a) studied foliar production of terpenes by *Ageratina adenophora* (Asteraceae, crofton weed), a Central and North American herbaceous perennial invasive in Asia (Fig. 1b). Seeds from different populations in native (Mexico) and non-native (China and India) areas were grown in a common garden and aboveground emission of terpenes was measured. Invasive

populations from India and China emitted more monoterpenes, 2-carene (Fig. 2d, upper panel), and α -phellandrene, which supports the novel weapons and shift-in-defence hypotheses (SDH; Box 2). However, the foliar emission of the monoterpene β -pinene (Fig. 2d, lower panel) and three sesquiterpenes ((E)- β -caryophyllene, (E)- α -bergamotene, and bicyclogermacrene) from *A. adenophora* was greater in its native range, supporting EICA. In another study, genotypes of invasive populations of *Solidago altissima* (Asteraceae, tall goldenrod) from Japan had greater production of five polyacetylenes in their roots and leaves and lower amounts of three diterpene acids than North American genotypes in their native range (Uesugi & Kessler, 2016). Biogeographic variation in chemical production by an NIS in its native and non-native ranges suggests a trade-off between costly vs less costly chemicals that provides competitive advantages for NIS against enemies in its new community, as predicted by EICA. When NIS escape from specialist enemies, they may reallocate resources to growth, reproduction, storage, or to producing less costly chemicals that protect against generalist enemies as predicted by the shift-in-defence hypothesis (SDH; Box 2; Doorduyn & Vrieling, 2011; Inderjit, 2012).

By contrast, some studies do not fully support NWH. For example, *Impatiens glandulifera* (Balsaminaceae, Himalayan balsam), an herbaceous annual native to the western Himalayas, is invasive in Europe where it negatively impacts native biodiversity (Hejda & Pyšek, 2006; Table 1). Ruckli *et al.* (2014) identified a quinone (2-methoxy-1,4-naphthoquinone; 2-MNQ) from its root exudates and leaf leachates and argued that this chemical plays an important role in its invasive success. In one experiment, Gruntman *et al.* (2016) tested whether the co-occurring species, *Urtica*

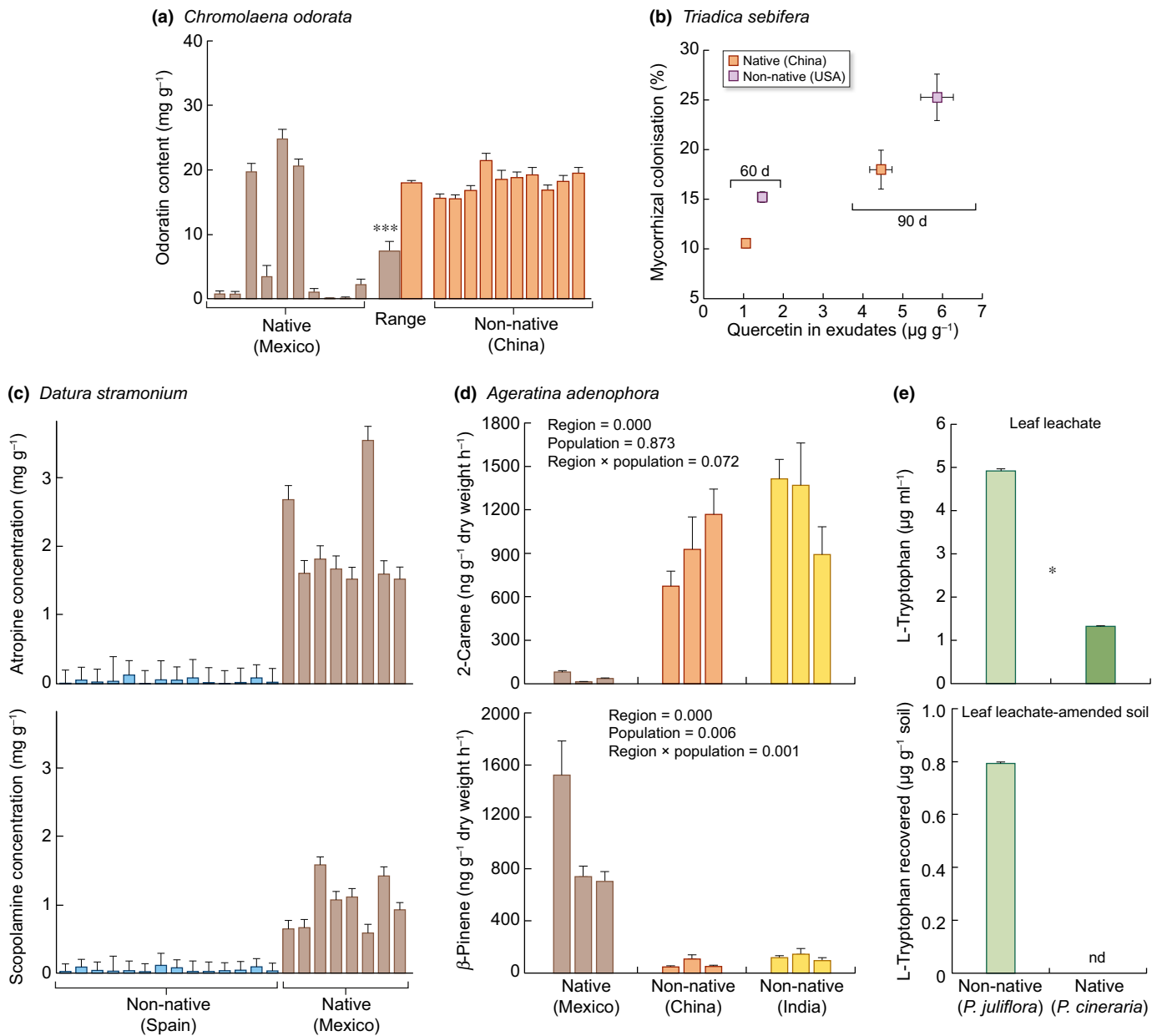


Fig. 2 Comparison of amounts of novel chemicals produced by non-native invasive species in non-native ranges compared with native ranges or to its native congener and its associated soil. (a) *Chromolaena odorata*, an aggressive invasive species, produced higher amounts of a chalcone odoratin in its introduced (China) range than in its native (Mexico) range (Zheng *et al.*, 2015). (b) Mycorrhizal colonisation and quercetin in root exudates of 60-d-old and 90-d-old *Triadica sebifera* plants from its native (China) and non-native (USA) populations. (c) Average concentration of two defence chemicals, atropine (upper panel) or scopolamine (lower panel), produced by *Datura stramonium* in its native (Mexico) and non-native (Spain) populations (Castillo *et al.*, 2019). Production of these two defence chemicals by *D. stramonium* was higher in the native range than its introduced range. (d) Differences in production of terpenes by the invasive forb *Ageratina adenophora* between its native (Mexico) and introduced (China and India) ranges (Inderjit *et al.*, 2011a). Litter of *Ageratina adenophora*, a Mexican invader in Asia, produces higher amounts of certain monoterpenes (e.g. 2-carene, upper panel) in its introduced range compared with its native range in Mexico, but the production of certain terpenes such as β -pinene (lower panel) was higher in the native range (Inderjit *et al.*, 2011a). (e) *Prosopis juliflora*, an aggressive invader in the arid, semiarid and saline areas of the world, produces L-tryptophan (Nakano *et al.*, 2003). The native congener of the invader, *Prosopis cineraria* produces L-tryptophan in smaller amounts and could not accumulate it in its soil (Kaur *et al.*, 2012). L-Tryptophan concentrations ($\mu\text{g ml}^{-1}$ leaf leachate) in *Prosopis juliflora* leaf leachates were 73.1% greater than those of *P. cineraria* (upper panel). A recovery of c. 40% L-tryptophan of the soil-added *P. juliflora* leachate was observed from the soil immediately after application, but we could not detect L-tryptophan in soil infiltrated with *P. cineraria* leachates (lower panel) (Kaur *et al.*, 2012). Reproduced with permission.

dioica (Urticaceae, stinging nettle), from the non-native range of *I. glandulifera* is more sensitive to its novel chemicals than *U. dioica* from the native range of the invader. Seeds of *U. dioica* were

collected from both the native and non-native ranges of *I. glandulifera*, while leaf extracts of *I. glandulifera* or soil conditioned by the invader were used only from the non-native range. This

study revealed no difference in the response of *U. dioica* (from the native or non-native range of *I. glandulifera*) to the effects of either the leaf extracts or *I. glandulifera*-conditioned soil and therefore does not support the NWH.

In the event that an NIS produces a chemical that is not novel for the invaded communities but is now in significantly higher concentrations and, if this chemical accumulates sufficiently in the environment, it can still affect the invaded ecosystem and communities. For example, L-tryptophan is produced by the NIS, *Prosopis juliflora* (Fabaceae, mesquite) in India, where its native congener, *P. cineraria*, also produces L-tryptophan but in much lower concentrations (Fig. 2e, upper panel; Kaur *et al.*, 2012). Soils in which *P. juliflora* grows accumulate appreciable amounts of L-tryptophan, but this is not the case in *P. cineraria* soils (Fig. 2e, lower panel; Kaur *et al.*, 2012). Here, L-tryptophan produced by *P. juliflora* may be considered a novel chemical because native residents experience high concentrations of L-tryptophan following *P. juliflora* invasion. The possibility that chemicals may be produced by an NIS and its native congeners could be considered a refinement of the NWH because of the addition of increased

production of existing chemicals. The NWH predicts that NIS bring chemicals novel to the invaded area. In addition to providing examples that support the NWH, we have proposed to expand and refine it. Variation in chemical production by a species between its native and non-native ranges can also explain cases of novel weapons, by virtue of SDH and EICA, and should be considered a corollary to the NWH (Inderjit *et al.*, 2011b; Gruntman *et al.*, 2016). We refine the NWH by including greater chemical production by an NIS relative to that of native congeneric species.

III. Novel chemical(s)-mediated mechanisms underlying invasion hypotheses

Novel chemicals introduced by NIS are broadly implicated in hypotheses invoking novel weapons or disruption of mutualistic associations. However, our understanding of the nuanced role of novel chemicals in interactions with key ecological factors is rudimentary. Novel chemicals orchestrate ecological, physiological, and evolutionary mechanisms that underpin the negative performance of native plants or facilitate growth of NIS (Fig. 3).

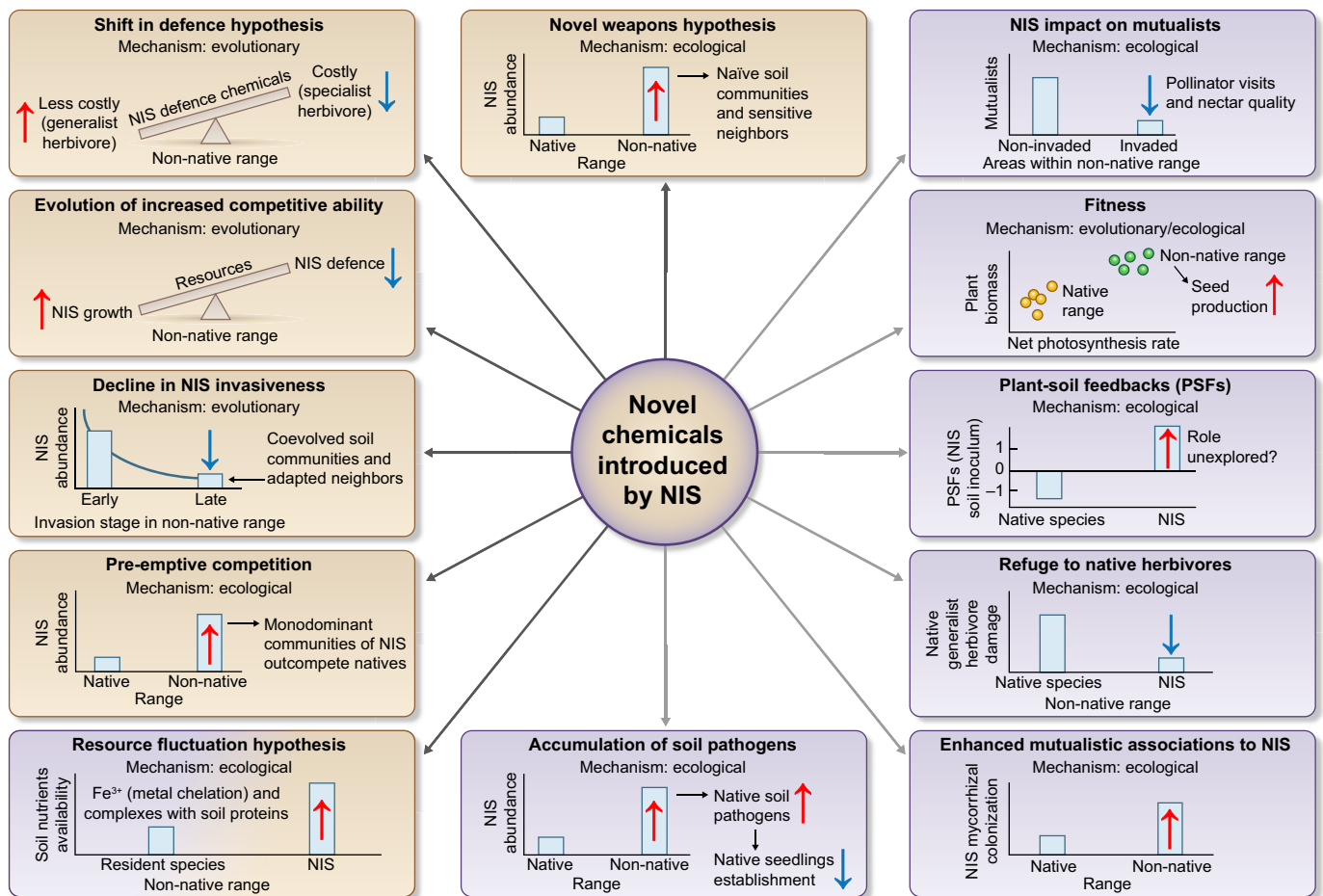


Fig. 3 The novel chemicals–invasion link to recognise that novel chemicals mediate physiological and ecological mechanisms underlying invasion hypotheses. Currently novel chemicals are largely studied in the context of the novel weapons hypothesis, evolution of increased competitive ability hypothesis, shift-in-defence hypothesis, pre-emptive competition, and disruption of mutualistic associations hypothesis (almond boxes). Novel chemicals indirectly involved in mechanisms underlie invasion hypotheses, including plant–soil feedbacks, impact on mutualists, accumulation of native soil pathogens, fitness, apparent competition, nutrient fluctuation, and availability, and/or defence against native herbivores (purple boxes). Red arrows indicate higher values. Blue arrows indicate lower values. NIS, non-native invasive species; PSFs, plant–soil feedbacks.

Through conceptual unification of theoretical and empirical data, the synergistic role of novel chemicals in mediating mechanisms of various invasion hypotheses can be unravelled. Below we discuss how novel chemicals can mediate ecological and evolutionary mechanisms underlying invasion hypotheses (Fig. 3).

1. Pre-emptive competitive advantages of NIS

Many NIS (e.g. *Chromolaena odorata* (Asteraceae; Fig. 1a), *Ageratina adenophora* (Asteraceae; Fig. 1b), *Alliaria petiolata* (Brassicaceae, garlic mustard; Fig. 1c), *Prosopis juliflora* (Fabaceae, mesquite; Fig. 1d)) form monodominant communities and suppress surrounding vegetation (Lankau *et al.*, 2009; Inderjit *et al.*, 2011a; Kaur *et al.*, 2012; Qin *et al.*, 2013; Zheng *et al.*, 2015) in part by producing novel chemicals (Table 1) that give the NIS a pre-emptive competitive advantage. Novel chemicals provide competitive advantages to the NIS against resident communities if native neighbours or their root symbionts are sensitive to these chemicals and naïve soil microbial communities cannot degrade them, as predicted by the NWH (Callaway & Ridenour, 2004). The key role of novel chemicals in an invasion mechanism is elegantly exemplified by the Japanese red alga *Bonnemaisonia hamifera* (Bonnemaisoniaceae), which is invasive in Scandinavia and suppresses establishment of green, brown, and red macroalgae by releasing 1,1,3,3-tetrabromo-2-heptanone (Svensson *et al.*, 2013), a novel chemical in Scandinavia (Enge *et al.*, 2012). The inability of native algae to establish near *B. hamifera* provides the invasive alga with a competitive advantage.

A community dominated by an NIS could maintain the relevant chemical pool in the environment by its periodic replenishment, therefore creating conditions for pre-emptive competition by reducing interspecific competition from resident species. Novel chemicals may not be important when NIS abundance is low, rendering their effects conditional (Kaur *et al.*, 2014). The production and activities of novel chemicals can vary among genotypes of the same species or in response to conspecific vs heterospecific communities. For example, genetic variation in sinigrin (a glucosinolate) concentration in the annual invader *Brassica nigra* (Brassicaceae, black mustard) determines relative outcomes in interspecific and intraspecific competition (Lankau, 2008). Genetic lines of plants with low sinigrin concentrations compete well against conspecifics but poorly against other species. By contrast, plants with high sinigrin concentrations compete strongly against heterospecifics but weakly against conspecifics, suggesting an evolutionary trade-off. As *B. nigra* plants with high sinigrin levels become dominant in the community by suppressing other species, selection begins to favour plants with low sinigrin concentrations, leading to decreased *B. nigra* dominance.

Inclusion of both naïve and experienced individuals of native species in non-invaded areas (i.e. individuals that have never experienced the NIS and those that have grown with them) in bioassay experiments can help elucidate adaptation of local species (Deck *et al.*, 2013). Experiments are needed to quantify the growth response of individual resident species to chemicals introduced by NIS and to identify species that are sensitive or resistant to novel

chemicals. Such data would be useful in restoration and conservation programmes.

2. Interference with physiology of native species

Plants allocate resources to costly enemy defence in their native range, including proteinase inhibitors (antidigestive proteins), polyphenol oxidases (antinutritive enzymes), or toxic compounds (alkaloids, terpenoids, phenolics) (Inderjit, 2012). It is often assumed that most NIS in their non-native ranges are largely free from specialist herbivores or pathogens at least during early invasion stages (ERH; Keane & Crawley, 2002). NIS, therefore, do not need to allocate resources to defence against specialist enemies, giving them a competitive advantage. This is the basis of EICA (Fig. 3; Blossey & Nötzold, 1995; Inderjit, 2012).

The hypothesis on evolutionary trade-offs for resource (nitrogen) allocation to growth (photosynthesis) vs defence (cell wall proteins) was tested for the NIS *Ageratina adenophora* (Feng *et al.*, 2009). Plants were grown in a common garden from *A. adenophora* seeds collected in its native range (Mexico) and non-native range (India and China). Invasive populations indeed had lower production of cell wall proteins, a lower ratio of cell wall proteins to total leaf proteins, and lower proportions of leaf N allocated to cell walls (Feng *et al.*, 2009), suggesting that invasive *A. adenophora* populations increase nitrogen allocation to photosynthesis and reduce allocation to cell wall proteins. Furthermore, invasive *A. adenophora* populations with high allocation to leaf nitrogen also exhibited higher photosynthetic energy use efficiency (PEUE) and they take less time to pay back leaf construction costs through photosynthesis (Feng *et al.*, 2011). Higher PEUE and shorter payback time in invasive *A. adenophora* populations compared with native *Ageratina* populations resulted in vigorous growth of invasive populations, supporting EICA. *Alliaria petiolata* (Brassicaceae, garlic mustard) in its non-native range, North America, expressed significantly higher photosynthetic rates (50%) in unfenced plots relative to plots that were fenced to exclude white-tailed deer (*Odocoileus virginianus*) (Heberling *et al.*, 2017). This difference was due to higher light intensities reaching the forest floor in unfenced areas driven by high herbivore pressure on native species, but not on *A. petiolata*, which is unpalatable to deer.

An interesting but largely unanswered question is whether native species would behave similarly to non-native species in the absence of specialist enemies. Uesugi & Kessler (2013) compared the competitive ability of eastern North American native *Solidago altissima* against the NIS *Poa pratensis* (Poaceae, bluegrass). Insecticide-treated and untreated control plants of *S. altissima* were propagated and resultant clones were used in a common garden experiment. Release from herbivory of the native *S. altissima* resulted in improved growth and greater production of polyacetylene compounds that suppressed *P. pratensis*, therefore providing *S. altissima* with a competitive advantage over *P. pratensis*. This example suggests that any species, whether native or NIS, when released from enemies could increase its competitive ability. However, most studies on the ERH and EICA are carried out with NIS because natives are unlikely to be released from their enemies. More evidence is needed to show that native species can

respond similarly to NIS in the absence of specialist enemies, and the ERH and EICA should also be tested on native species with herbivores experimentally excluded for long periods.

3. Reduced herbivory on NIS

Absence of specialist enemies in the invaded range provides a competitive advantage to NIS at least during early invasion phases (Keane & Crawley, 2002). NIS therefore tend to invest less in costly constitutive defence chemicals and more in producing less costly inducible defences (Box 2; SDH, Doorduyn & Vrieling, 2011), which may also act as novel chemicals. For example, in the non-native range of *Brassica nigra*, increased levels of inducible glucosinolates (sinigrin) correlate negatively with damage by grey garden slugs (*Agrilolimax reticulatus*), a generalist herbivore, but positively with damage by the specialist aphid *Brevicoryne brassicae* (Lankau, 2007). Other research has shown that invasive *Brassica* species shifted from producing costly constitutive trypsin inhibitors to less costly defence chemicals such as glucosinolates (Cipollini *et al.*, 2005). More studies are needed that integrate laboratory and field studies to demonstrate shifts from costly to less costly defence chemicals in response to lack of specialist enemies in the non-native range and to determine whether such shifts confer a competitive advantage to the NIS.

Our understanding of the role of novel chemicals in mediating certain competitive interactions such as apparent competition is very limited, but novel chemicals can potentially drive these interactions. For example, a native generalist herbivorous isopod, *Idotea granulosa*, promotes invasion by the Pacific Ocean native macroalga, *Bonnemaisonia hamifera*, into the Atlantic Ocean. Although *B. hamifera* is competitively inferior to native macroalgae including *Lomentaria clavellosa*, *Ceramium virgatum*, and *Polysiphonia fucooides*, it dominates by providing a refuge from fish predation for the native generalist (Enge *et al.*, 2013). This protection causes the native isopod to consume more of the native algae, promoting *B. hamifera* invasion. The generalist, *I. granulosa*, avoids feeding on *B. hamifera* because the alga produces 1,1,3,3-tetrabromo-2-heptanone, rendering it less palatable (Enge *et al.*, 2012, 2013). This example demonstrates the potential for a native herbivore and a novel chemical interaction to drive the dominance of an otherwise competitively inferior NIS over native macroalgae. Similarly, ungulates may prefer native plant species over NIS because novel chemicals are present, conferring a competitive advantage to the NIS. White-tailed deer, *Odocoileus virginianus*, found *Alliaria petiolata* unpalatable probably due to the presence of glucosinolates and did not consume it, but high deer herbivory levels were observed on co-occurring *Trillium grandiflorum* and other native understory perennial species that compete with *A. petiolata* (fig. 1 in Kalisz *et al.*, 2014; Heberling *et al.*, 2017). When deer are excluded, fitness of *A. petiolata* declined, while fitness of *T. grandiflorum* and the other native understory perennial species increased. These results suggest that white-tailed deer mediate competitive interactions between unpalatable *A. petiolata* and native species to favour the invader. More empirical studies are needed to understand how herbivores alter ecological functions of novel chemicals.

4. Disruption of mutualisms

Mycorrhizal fungi Previous studies have shown that novel chemicals can disrupt mutualistic interactions between mycorrhizal fungi and native species (Stinson *et al.*, 2006; Callaway *et al.*, 2008; Hale *et al.*, 2011; Hale & Kalisz, 2012; McCary *et al.*, 2019). For example, mycorrhizas were less abundant in soil in field plots invaded by *A. petiolata* than in soil of uninvaded plots (Cantor *et al.*, 2011). Furthermore, plants of AMF-dependent native species when grown in soil treated with litter of *A. petiolata* had lower photosynthetic rates and stored less carbon than control plants grown in soil treated with litter of *Hesperis matronalis* (Brouwer *et al.*, 2015). Glucosinolates released by *A. petiolata* probably disrupt mutualistic associations between AMF and roots of native species (Hale *et al.*, 2011; Brouwer *et al.*, 2015; Gilliam, 2015). Glucosinolates can be transformed into more toxic isothiocyanates in the presence of the enzyme myrosinase (Cantor *et al.*, 2011; Hale *et al.*, 2011). Data quantifying soil concentrations of myrosinase, isothiocyanates, and glucosinolate are scarce, and how these chemicals disrupt mutualistic associations between native species and mycorrhizal networks in native vs non-native ranges is not well understood. These studies are restricted to a few NIS from a generally non-mycorrhizal family, Brassicaceae, so the results may be due to family-specific characteristics (but see Meinhardt & Gehring, 2012).

Invader-mediated loss of mutualistic networks may alter chemical interactions among native species as well. For example, some native species produce chemicals (e.g. juglone in *Juglans* spp.; Willis, 2000) at phytotoxic levels that give them a competitive advantage. AMF hyphae have been shown to transfer juglone to roots of the receiver plant (Achatz *et al.*, 2014; Achatz & Rillig, 2014). Disruption of mycorrhizal networks in native species could reduce the transfer of chemicals to other species and lower their negative effects. We have scant insight into whether novel chemicals suppress mycorrhizas in ways that lower the impact of native species.

Novel chemicals have also been reported to enhance mycorrhizal associations of NIS (Tian *et al.*, 2021). The rapidly growing tree *Triadica sebifera* (Euphorbiaceae, Chinese tallow) is invasive in North America and native in China. It produces a root-exuded flavonoid (quercetin) in higher concentrations in its non-native range than in its native range (Tian *et al.*, 2021), which helps in establishing greater mycorrhizal colonisation of *T. sebifera* in the non-native range (Fig. 2b). More biogeographic studies of other NIS are required to test the generality of the hypothesis that novel chemicals mediate the establishment of mutualistic associations more often in non-native ranges of NIS.

Pollinators Novel chemicals can reduce pollinator visits or nectar production of native species (Strauss *et al.*, 1999; Adler *et al.*, 2012; Hale & Kalisz, 2012). Chemicals present in NIS nectar may negatively affect pollinators. For example, chemicals (i.e. grayanotoxin I and III) present in nectar of *Rhododendron ponticum* (Ericaceae, common rhododendron), which is invasive in the United Kingdom, negatively affect certain pollinators (Tiedeken *et al.*, 2016). Furthermore, if NIS that emit high concentrations of volatile chemicals dominate native communities, these volatiles

could mask or dilute floral scents produced by native species or even repel pollinators (Hale & Kalisz, 2012). For example, volatile chemicals produced in response to herbivory of a native species can reduce visits of a native pollinator. In its native range in the Peruvian Andes, the wild tomato, *Solanum peruvianum* (Solanaceae) releases volatile chemicals in response to attack by a beetle (*Epitrix* potato flea beetle), which reduces pollinator visitation, adversely affecting seed production (Kessler *et al.*, 2011).

NIS that have escaped from specialist enemies early during an invasion may attract more pollinators in the non-native range, as the plants can be more vigorous there. The Eurasian native *Pastinaca sativa* (Apiaceae, wild parsnip) was introduced to the USA almost 300 yr ago. Its specialist herbivore, the parsnip webworm (*Depressaria pastinacella*), was introduced 150 yr ago and these two species have coevolved in the USA. Interestingly, in New Zealand, another introduced range, *P. sativa*, has only recently been exposed to the parsnip webworm (Zangerl *et al.*, 2008; Jogesh *et al.*, 2013). A study comparing *P. sativa* from the USA and New Zealand found that the New Zealand plants had more pollinator visitations and higher seed set than those from the USA, due to greater production of terpenes that promote pollinator visits (Jogesh *et al.*, 2013). More pollinator visits to *P. sativa* in New Zealand suggested that pollination can be influenced as envisioned in the ERH at least early in an invasion. Although this study did not invoke a role for novel chemicals, biogeographic comparisons of the release of terpenes by *P. sativa* may help to determine the role terpenes play in attracting more pollinators, which further contributes to higher seed production by *P. sativa*.

Interactions among mutualists We poorly understand how belowground processes (nutrient fluctuations and mutualistic associations) affect nectar quality or floral visits. In general, litter input can increase nectar sugar content (Baude *et al.*, 2011). Given that pollinator visits and seed set of *Chamerion angustifolium* (Onagraceae, fireweed) were higher in AMF-hosting plants than in non-AMF plants (Wolfe *et al.*, 2005), loss of AMF function via novel chemicals of an NIS could depress native plant fitness. Furthermore, experimentally induced loss of AMF within patches in a plant community has adversely influenced the types of pollinators and number of floral visits made to the patch, primarily by suppressing floral display (Cahill *et al.*, 2008). This result implicates resource stress and fitness declines of native plants as a mechanism of invasion success when novel chemicals reduce AMF function. Additionally, lower quality and or quantity of nectar produced by native plants without their AMF could adversely affect their pollination prospects, as production of nectar and pollen depends upon the plants' carbon assimilation potential (Hale & Kalisz, 2012).

5. Facilitation via soil nutrient availability

Another insufficiently examined mechanism involving novel chemicals is how they may manipulate soil nutrients (Ehrenfeld, 2003; Allison & Vitousek, 2004; Meisner *et al.*, 2012). NIS forming monospecific stands may have better access to resources than when they are growing in species-diverse less invaded areas (Teixeira *et al.*, 2020). Novel chemicals can facilitate the uptake of

soil nutrients or metal ions, providing competitive advantages to NIS against resident communities (Tharayil *et al.*, 2009). For example, 8-hydroxyquinoline (a quinoline) exuded by roots of a Eurasian invader in North America, *Centaurea diffusa*, forms a non-toxic complex with iron in the soil (Tharayil *et al.*, 2009). Because iron is an important micronutrient required for photosynthesis and other physiological processes, the uptake of iron from infertile soils confers a competitive advantage to *C. diffusa* (Tharayil *et al.*, 2009). High resource use efficiency in terms of carbon assimilation per unit of resource can be a strategy of NIS in resource-poor environments (Funk & Vitousek, 2007). The generality of these results and the potential for novel chemicals to increase resource use efficiency of other NIS require further study.

Plant-released chemicals may facilitate the release of nutrient ions into soil solutions by microbial activities and/or by forming complexes with metal ions or organic compounds (Appel, 1993). Data on the effect of novel chemicals on soil nutrient availability are scarce, particularly on nitrogen availability in native and non-native ranges. Previous studies, however, showed an increase in soil nutrients, for example nitrogen, in response to invasion (Ehrenfeld *et al.*, 2001; Ehrenfeld, 2010). This increase results in NIS-mediated resource fluctuations, which give competitive advantages to the NIS as predicted by the 'fluctuating resource hypothesis' (FRH) (Box 2; Davis *et al.*, 2000). Some NIS accumulate chemical-rich litter under their canopies, which can influence local soil nutrient availability (Facelli & Pickett, 1991; Elgersma & Ehrenfeld, 2011). Litter from an NIS might create abiotic or biotic soil legacies that can aid the NIS itself and its neighbours by increasing nutrient mineralisation and availability (Meisner *et al.*, 2012). Litter decomposition in local or 'home' soil can rapidly alter soil chemistry (i.e. nutrient levels and chemical compounds), and this alteration can benefit the plant or other conspecific individuals, a phenomenon called 'home-field advantage' (Wallenstein *et al.*, 2013; Austin *et al.*, 2014). Input of litter in the home environment over longer time periods can select for soil microorganisms that rapidly degrade this litter (Vivanco & Austin, 2008). More evidence is needed to establish how novel chemicals influence litter degradation in native vs non-native ranges. Some NIS may enhance nutrient availability indirectly by disrupting mutualistic associations of native species, therefore preventing nutrients from being channelled to native seedlings via mycorrhizas. In southwestern USA, non-native tamarix (*Tamarix* spp., Tamaricaceae) suppresses mycorrhizas, disrupting provision of nutrients to native *Populus fremontii* (Salicaceae, Fremont's cottonwood), ultimately resulting in increased nitrate-N levels (Meinhardt & Gehring, 2012).

Some species (e.g. wattles (*Acacia mearnsii* and *A. dealbata*, Fabaceae)) invasive in Europe and Asia and invasive pines (Pinaceae) in the Southern hemisphere contain large amounts of condensed tannins in their older needles/leaves and litter (Hättenschwiler & Vitousek, 2000). Under controlled conditions, condensed tannins may form complexes with soil proteins, yielding dissolved organic nitrogen (DON) (Hättenschwiler & Vitousek, 2000; Jones *et al.*, 2004; Joannise *et al.*, 2009; Adamczyk *et al.*, 2013). The question to be answered is how such tanniferous species take up DON (i.e. tannin-protein complexes). Although several studies have suggested that tanniferous species can take up DON,

probably through their mycorrhizas (Hättenschwiler & Vitousek, 2000; Adamczyk *et al.*, 2013), well replicated field studies are lacking. The catabolic abilities of soil microorganisms may differ in native vs non-native soils (Marchante *et al.*, 2008). For example, chemicals present in leachates of species such as *A. dealbata* (silver wattle) in their non-native ranges reduce soil bacterial diversity in pine but not oak forests (Lorenzo *et al.*, 2013), which could result in differential nutrient accumulation in these two forest types. In another example, soil enriched by nitrogen benefits both *Rhamnus cathartica* (buckthorn, Rhamnaceae), which is native in Europe and Asia and invasive in North America, and the European earthworm *Lumbricus terrestris*, invasive in North America (Roth *et al.*, 2015). Apparently, buckthorn and the earthworm facilitate each other's invasion (Eisenhauer *et al.*, 2012). Buckthorn litter contains more nitrogen, and earthworms decompose buckthorn litter faster than that of native species in their non-native range (Heneghan *et al.*, 2002). Buckthorn can displace native species by obstructing light, by soil acidification, and by enhancing soil nitrogen levels as the result of litter decomposition (Heneghan *et al.*, 2002). Buckthorn produces an anthraquinone, emodin (Sacerdote & King, 2014), but further empirical evidence is needed to establish whether this is a novel chemical and to study its effects on performance of native plant species and on earthworms and its impacts on soil properties.

6. Decline in novel chemical production with longer invasion history

An important question is whether novel chemical concentrations in recently invaded areas exceed those in areas invaded longer ago. In *Alliaria petiolata*-invaded sites that had a longer invasion history, population mean concentrations of novel chemicals (glucosinolates) within *A. petiolata* were lower than in recently invaded sites (Lankau *et al.*, 2009). A decline over time in production of a chemical first introduced by an NIS in the early phases of the invasion has also been shown for *Mikania micrantha* (Asteraceae, bitter vine) (Huang & Peng, 2016). A higher density and abundance of native species may result in greater chemical production by an NIS as an evolutionary response to higher densities of heterospecific competitors. Sinigrin production by invasive *A. petiolata* was higher when plants were exposed to high densities of native neighbours (Lankau, 2012). Interestingly, certain traits of native species can provide competitive advantages against an invader. A native forb, *Pilea pumila*, from high sinigrin sites has higher fitness when invader abundance is high than when it is low (Lankau, 2012). These results suggest that both the native species and an NIS can evolve in response to invasion. Over time, populations of local enemies in the invaded range may also evolve or enemies from the home range may be introduced and these changes can stimulate reallocation of resources away from growth to defence as in a plant's native range (Lankau, 2012). This possibility highlights the importance of determining, or at least acknowledging, invasion history of invaded communities and the role of invader evolution during the invasion process. Common garden experiments with seeds collected from invaded ranges with varying times since invasion can help us to evaluate variations in novel chemical production. Such experiments would also help clarify

differences in chemistry, defence against herbivores, resource allocation to defence or production of novel chemicals, and their impact on local species in sites with varying invasion history, and to determine which mechanisms are changing over invasion history across more NIS.

7. Synthesis

Linking research on the NWH, SDH, and EICA would elucidate the role of novel chemicals in mechanisms of altering physiology of native species (see Feng *et al.*, 2009; Inderjit *et al.*, 2011b; Zheng *et al.*, 2015). Chemical–plant–microbe interactions should be investigated within the context of chemical-mediated competitive abilities of natives vs NIS. Our knowledge is limited on how declines in novel chemical production influence pollinator visits, herbivore damage, pathogen attack, seed production, plant–soil feedbacks, and mutualistic interactions in native communities, and fitness traits of NIS. Evolved declines in novel chemical production over time may help to explain why NIS that co-occur with native species for long periods have more diverse pollinator visitors than do recently invading NIS (Pyšek *et al.*, 2011). Novel chemicals are currently largely known for their role in NWH and EICA and indirectly for their role in disrupting mutualistic associations (Inderjit *et al.*, 2011a,b; Zheng *et al.*, 2015) (Fig. 3). Here we argue that novel chemicals can interact with invaded communities and can explain variation in fitness, apparent competition, decline in invasiveness, facilitation of soil nutrient availability, accumulation of native soil pathogens, and/or defence against native herbivores (Fig. 3). Evidence suggests linkages between soil microbial communities and plants (Inderjit, 2005; Inderjit *et al.*, 2011b), and it is therefore reasonable to predict that novel chemicals can be the key component of a mechanism for plant–soil feedbacks (PSFs) experienced by NIS. Clearly no single mechanism explains all plant invasions (see Lau & Schultheis, 2015). However, we propose that novel chemicals play an important role in a large number of invasion hypotheses, directly or indirectly (Fig. 3).

IV. Linkages among novel chemicals, soil microbial communities, mutualists, and plant enemies

Interactions among the soil microbial community, plant chemistry, and plant enemies influence overall plant performance (van der Putten *et al.*, 2001; Inderjit *et al.*, 2011b; Veen *et al.*, 2019). However, we lack an adequate understanding of how linkages among plant chemistry, soil microbial communities, and plant enemies facilitate NIS performance. Three-way interactions among novel chemicals, soil biota, and enemies may play out differently in native and non-native ranges, through differences in biogeographic-evolutionary advantages, that is evolved relationships among soil microbial communities, plant enemies, and plant chemicals (Callaway & Ridenour, 2004; Hierro *et al.*, 2005; Inderjit *et al.*, 2011b). We predict strong interactions among plant chemistry, soil microbial communities, pollinators, and herbivores in novel ranges, and that novel chemicals, PSFs, and defence or resistance to herbivores are interlinked (see Biere & Bennett, 2013). For example, leachate from NIS can favour the growth of certain

fast-growing bacteria (Lorenzo *et al.*, 2013), which can influence PSFs. Plant chemicals can influence abundance and diversity of soil microbes (Kaur *et al.*, 2009; Inderjit *et al.*, 2011b), and soil microbes can influence the fate and functions of those chemicals (van der Putten *et al.*, 2001; Inderjit, 2005). One possible outcome of interactions between chemicals and soil microbial communities is that resources fluctuate through changes in litter decomposition (Austin *et al.*, 2014). We present a framework that links various novel chemical-mediated ecosystem attributes such as competitors, plant enemies, soil microbes, mutualists, and soil nutrients (Fig. 4). Our framework will help to unravel linkages among novel chemical-driven invasion mechanisms and highlights the need to study them.

Volatile compounds released by an NIS during induced defence against herbivores may discourage pollinators (Hale & Kalisz, 2012), which could affect seed set (Kessler *et al.*, 2011), and the damage herbivores inflict on plant tissues could affect mutualistic associations between plants and pollinators (Glaum & Kessler, 2017; Jacobsen & Raguso, 2018). We provide two examples showing how PSFs can influence plant defence against herbivores.

Jacobaea vulgaris (Asteraceae, ragwort) is an early successional species that colonises disturbed soil and can dominate in its native range in Eurasia (van de Voorde *et al.*, 2012). It experiences strong negative conspecific PSF, but its performance is also greatly reduced by soil-mediated effects of heterospecific neighbours. These conspecific and heterospecific PSFs influence its production of amino acids and pyrrolizidine alkaloids, which in turn, influences herbivore performance (Kos *et al.*, 2015; Kostenko *et al.*, 2017). Whether *J. vulgaris* exhibits a negative PSF in its invasive range is unknown. Because this species is highly sensitive to changes in the soil microbial community and responds negatively to soil conditioning by other species (van de Voorde *et al.*, 2012; Wang *et al.*, 2019), plant–soil interactions are not likely to be the reason *J. vulgaris* becomes invasive. Further evidence is needed on whether reduced herbivory is the cause. Interestingly, alkaloid patterns of non-native and native populations of *J. vulgaris* can greatly differ (Lin *et al.*, 2015), and more research is needed to disentangle interactions among alkaloids, soil microbes, and aboveground herbivores. Our second example compares the effect of soil pathogens and herbivores on *Tanacetum vulgare* (Asteraceae, tansy,

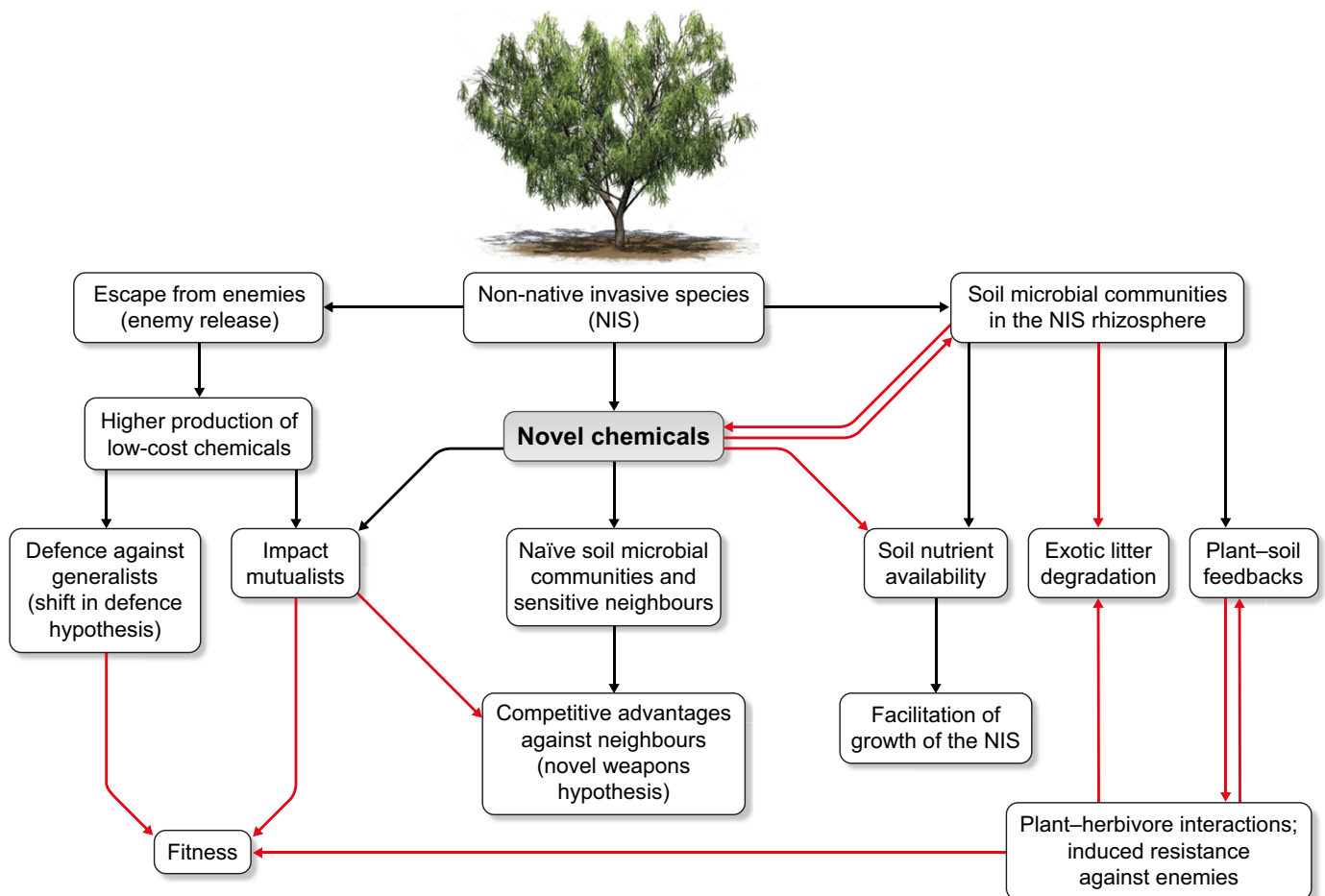


Fig. 4 Framework representing linkages occurring in invasions that are mediated by novel chemicals produced by NIS. Novel chemicals affect introduced communities including soil biota, plant enemies, soil nutrients, competitors, and mutualists, which results in changes in linkages. Links among some of the invasion hypotheses for example novel weapons, evolution of increased competitive ability, and shift-in-defence hypothesis are known to a limited extent (shown by black arrows). Currently, there is too little evidence to link other invasion hypotheses (shown by red arrows). The proposed framework visualises linkages among several invasion hypotheses. NIS, non-native invasive species.

native in Europe and introduced to North America) and *Solidago gigantea* (native to North America and introduced to Europe) in their native and introduced ranges (Lucero *et al.*, 2020). *Solidago gigantea* escaped the negative effects of soil biota but not damage by herbivores in Europe, and the reverse pattern was observed for *T. vulgare*.

Plant growth-promoting bacteria and mycorrhizae can improve plant performance and trigger induced resistance against insects (Pineda *et al.*, 2010, 2012). Mutualistic associations may therefore influence species-specific distributions of defensive chemicals in shoots and roots. Indeed, in the presence of AMF the relative distribution of cardenolides, toxic chemicals involved in defence against insects, shifted in aboveground vs belowground parts in different *Asclepias* species (Asclepiadaceae, milkweeds) (Vannette *et al.*, 2013). While foliar concentrations of cardenolides were affected most in certain species of *Asclepias*, root concentrations of cardenolides were unaffected. Such microbe–mutualist–competitor–plant enemies–novel chemical interactions need more exploration in native vs non-native ranges of NIS.

A recent study has shown that plant chlorogenic acid concentrations, soil microbial richness, and resistance to thrips are correlated (Pineda *et al.*, 2020). Plant chemistry-mediated changes in soil microbiomes can influence the resistance to aboveground insect herbivory of plants that initially inhabit a site and that of other plants that grow later in the soil, via microbe-induced changes in plant defence compounds. Other studies have shown that plant-mediated changes in soil microbial communities can also affect aboveground insect herbivores directly (Hannula *et al.*, 2019). The gut microbiome of insect herbivores such as caterpillars can be essential for digestion, pathogen suppression, and production of specific compounds. Plant-mediated changes in the soil microbiome can be reflected in the caterpillar microbiome even when no microbial changes are detected in the host plant microbiome (Kikuchi *et al.*, 2007; Hannula *et al.*, 2019). Therefore, changes in the soil microbiome due to novel chemistry of an NIS can alter plant–insect interactions via the effects of microbes on the plant, but also via microbe-mediated effects on herbivore microbiomes and herbivore performance that subsequently alter plant–herbivore interactions. Despite advances such as those described above, we have little understanding of how changes in soil microbial communities mediated by NIS can affect aboveground herbivory. As both soil microbes and defence against herbivores can be mediated by novel chemicals, it would be interesting to explore the linkages between positive PSFs mediated by NIS and reduced herbivory and to compare this phenomenon to reduced herbivory due to lack of enemies as predicted by the ERH.

Our framework for linkages among novel chemicals, competitors, soil communities, mutualists, plant enemies, and nutrient cycling would help to unravel the complexity of cross-talk among them (Fig. 4). For example, research is needed to understand how herbivore-free invaded communities affect the fitness of native species and if herbivore-free invaded communities reverse the high fitness of NIS. NIS may have higher resource assimilation abilities in non-native ranges compared with native ranges due to the lower allocation of resources to costly defence chemicals, at least early during invasion. Higher photosynthetic nitrogen-use efficiency

could contribute to invasion by NIS of low-resource habitats (Funk & Vitousek, 2007; Feng *et al.*, 2009), yet we lack research on whether higher growth rates or photosynthetic nitrogen-use efficiency could result in higher seed production by the non-native plant. A challenge is to design studies integrating the roles of novel chemicals, PSFs, and plant defence against enemies in plant invasion. Common garden experiments to study the interaction of PSFs, novel chemicals, and defence against enemies would be the first step to understand the three-way interactions among soil microorganisms, chemicals, and plant enemies in invasion. Such experiments would help us to understand how the introduction of novel chemicals by an NIS would affect the soil microorganisms associated with them, their native suppression potential, and defence against enemies. Previous studies have shown that chemicals can be transferred to fungal partners of the host plant and may play a role in defence against fungivores (Duhamel *et al.*, 2013). Loss of effectiveness of chemicals produced by native species may also lower the abundance of the species that produce them, because reduced transfer of chemicals by native species can lower their competitive ability and give an advantage to NIS.

Novel chemicals mediate interactions in the invaded communities among soil biota, plant enemies, soil nutrients, competitors, and mutualists. Lau & Schultheis (2015) discussed the potential for synergies that exist between mechanisms envisioned by different hypotheses. It is not yet possible to link processes involved in plant invasions such as plant–soil feedbacks, defence against enemies, facilitation via soil nutrients, fitness, and the impact of mutualists (Fig. 4). The proposed framework is a start to visualise several of these interactive processes and suggests a need for studying novel chemical-mediated invasion hypotheses interactively, not individually.

V. Concluding remarks and future research

The current perspective on the various roles novel chemicals play in invasions is narrow. By mediating species interactions and evolutionary responses, chemicals released by an NIS may influence community composition, and this will add a new dimension to invasion ecology. These chemically mediated interactions can differ substantially between the native and the non-native ranges of a species, suggesting the loss of coevolved relationships in the invaded ranges. If plants adapt to each other's chemistry, then such adaptations can provide a fresh look at the rules by which communities are assembled. Researchers are currently focusing on different aspects of novel chemicals with particular interest in studying their impact on community assembly. Studying the roles of novel chemicals in mechanisms that underpin invasion hypotheses is challenging and should entail multidisciplinary approaches and rapidly evolving tools in ecology, chemistry, and molecular biology. Future research should focus on the linkages between different invasion hypotheses including NWH, EICA, PSFs, FRH, and defence against enemies instead of investigating invasion mechanisms in isolation (Lau & Schultheis, 2015). We should ask: (1) how an NIS grown in the presence or absence of its soil microorganisms influences the production of novel chemicals; (2) how differences in the abundance and diversity of soil

microorganisms influence PSFs, affect production of chemicals, and provide competitive advantages to the NIS; (3) whether positive PSFs experienced by an NIS provide induced defence against enemies of the invasive species; and (4) how novel chemicals and soil microorganisms interact to affect litter degradation and therefore nutrient availability. Future research should integrate novel chemicals, PSFs, and defence against enemies through well replicated sites and attempt to develop model plants to test the novel chemical-mediated invasion hypotheses.

One difficulty in novel chemical research is the lack of direct evidence that release of a chemical affects the growth of neighbouring plants (Inderjit *et al.*, 2009). Although evidence exists for uptake of chemicals by cell-to-cell contact (Gross, 1999; Svensson *et al.*, 2013), such direct chemical uptake by plants is rarely shown in soil systems (but see Zhang *et al.*, 2015). One possible solution could be to manipulate plants genetically to silence production of a particular chemical. Genetically manipulated plants are extensively used in research on plant–plant and plant–herbivore interactions (see Baldwin *et al.*, 2006). Molecular tools could be used to silence or to overexpress genes responsible for synthesising a target chemical (e.g. sinigrin) through transformation (see Krügel *et al.*, 2002). Plant molecular research received a boost from the development of *Arabidopsis thaliana* as a model system. We lack a model plant to test invasion hypotheses mediated by novel chemicals. Although construction of transgenic lines does not seem possible for every invasive species, plants such as *B. nigra* and *A. petiolata* could be promising candidates. Transgenic plants could be used to study the ecological roles of novel chemicals at molecular levels.

Ecologists have noticed uneven and declining support for many major invasion hypotheses including the NWH (Jeschke *et al.*, 2012). One reason could be the dearth of research elucidating linkages between novel chemicals and various ecosystem processes and factors to understand invasion mechanisms, which hinders our understanding of novel chemicals in ecological and evolutionary contexts. Not all NIS produce novel chemicals that accumulate in the environment at biologically active concentrations. However, when present, such chemicals could directly or indirectly trigger major invasion pathways (Fig. 3), and this aspect is rarely studied. The challenge is to design field studies that incorporate habitat or site-specific characteristics, trait and phylogenetically based characteristics, and environmental variables that might influence chemical production and accumulation. The search for chemically driven routes that trigger major invasion mechanisms will be difficult. But responding to this challenge may strengthen our understanding of novel chemicals as a critical driver of plant invasion. Novel chemicals are largely studied for their roles in suppressing plant species, mutualists, and to some extent, the availability of soil nutrients. The roles of novel chemicals in competition, pollination, and native plant floral defences are not studied in depth, which is limiting progress in invasion biology.

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