



## Tansley review

# The emerging science of linked plant–fungal invasions

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## Summary

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Invasions of alien plants are typically studied as invasions of individual species, yet interactions between plants and symbiotic fungi (mutualists and potential pathogens) affect plant survival, physiological traits, and reproduction and hence invasion success. Studies show that plant–fungal associations are frequently key drivers of plant invasion success and impact, but clear conceptual frameworks and integration across studies are needed to move beyond a series of case studies towards a more predictive understanding. Here, we consider linked plant–fungal invasions from the perspective of plant and fungal origin, simplified to the least complex representations or ‘motifs’. By characterizing these interaction motifs, parallels in invasion processes between pathogen and mutualist fungi become clear, although the outcomes are often opposite in effect. These interaction motifs provide hypotheses for fungal-driven dynamics behind observed plant invasion trajectories. In some situations, the effects of plant–fungal interactions are inconsistent or negligible. Variability in when and where different interaction motifs matter may be driven by specificity in the plant–fungal interaction, the size of the effect of the symbiosis (negative to positive) on plants and the dependence (obligate to facultative) of the plant–fungal interaction. Linked plant–fungal invasions can transform communities and ecosystem function, with potential for persistent legacies preventing ecosystem restoration.

## I. Introduction

Invasions of alien species are both a component and a driver of global change, including loss of biodiversity, modification of carbon and nutrient cycles, and disruption of ecosystem services (Dickie *et al.*, 2011; Corbin & D'Antonio, 2012). Alien plants and fungi (including oomycetes for the purpose of this review) are prominent drivers of these changes (Desprez-Loustau *et al.*, 2007; Vilà *et al.*, 2011). However, while both plants and fungi are important groups of invasive species in their own right, the symbiotic interactions between them are critical determinants of their ecological and evolutionary impacts (Mitchell *et al.*, 2006; Pringle *et al.*, 2009). Obvious examples include the invasion of alien plant pathogens into new regions (e.g. sudden oak death *Phytophthora ramorum*, chestnut blight *Cryphonectria parasitica* and white pine blister rust *Cronartium ribicola* in North America, and ash dieback *Hymenoscyphus fraxineus* in Europe; Anagnostakis, 1987; Grünwald *et al.*, 2012; Cleary *et al.*, 2016) and co-invasion of fungal mutualists and their host plants (e.g. mycorrhizal fungi and Pinaceae in the Southern Hemisphere; Dickie *et al.*, 2010). Less obvious examples include enemy release following the introduction of plants into new regions (e.g. escape from enemies; Maron *et al.*, 2014) and disruption of mutualistic interactions (e.g. garlic mustard *Alliaria petiolata* suppressing mycorrhizas of native plants; Stinson *et al.*, 2006).

The aim of this review is to elucidate how plant–fungal symbioses, including positive and negative interactions (see

Table 1), can shape the invasion of both plants and their fungal symbionts and influence downstream effects, including trophic interactions, nutrient dynamics and ecosystem resilience. While there have been previous reviews of biotic interactions in invasions (Mitchell *et al.*, 2006; Amsellem *et al.*, 2017), these often deal separately with pathogens (Dunn & Hatcher, 2015; Blackburn & Ewen, 2016) and mutualists (Richardson *et al.*, 2000; Pringle *et al.*, 2009; Nuñez & Dickie, 2014). Yet both ‘pathogen’ and ‘mutualist’ are idealized end-points along a continuum of symbiotic interactions and previous reviews have not considered similarities across the continuum. Furthermore, there has been little integration of perspectives from across the disciplines of plant pathology, mycology and plant ecology. Here, we unify the interactions of fungal mutualists and pathogens with alien plants by focusing on the structure of interactions between species from different origins (native vs alien). We simplify complex interaction networks as interaction ‘motifs’, which are the simplest set of species necessary to describe a particular interaction structure and which form repeating patterns across interaction networks (Table 1). Based on these motifs, our synthesis aims to develop a conceptual approach for understanding the important role of plant–fungal linkages in invasion, so as to (1) unravel some of the complexity of understanding these interactions, (2) elucidate connections between the many different hypotheses proposed to date to explain biological invasions (Catford *et al.*, 2009) and (3) enable development of a framework for assessing the influence of plant–

**Table 1** Glossary of terms as used in this review; individual interaction motifs are named and defined in Tables 2 and 3

Term	Definition
Alien species	A species that has been introduced either deliberately or accidentally by humans into a region where it is not native, including spread from such regions. Synonym with ‘introduced’, ‘exotic’, ‘nonnative’ or ‘nonindigenous’ species (Pyšek <i>et al.</i> , 2004)
Apparent competition/facilitation	A generalized three-way interaction where one species affects the fitness of another species at the same trophic level through its effects on a third species
Invasive species	An alien species that reproduces and is capable of, or has, spread over wide areas (Pyšek <i>et al.</i> , 2004)
Linked plant–fungal invasion	Plant or fungal invasion where the success, failure, or impact of that invasion is substantially driven by a symbiotic interaction of the invasive species with fungi or plants, respectively
Motif	The minimum number of nodes (species or groups of species) and their linkages necessary to describe an interaction as a recurrent pattern within a broader interaction network
Mutualism	A symbiosis in which both partners receive a net benefit as a result of the interaction
Mutualist fungus	A symbiotic fungal species that is typically beneficial to plants, regardless of whether it can sometimes occur in other states (parasitic, commensal or saprotrophic). In this review, we primarily focus on mycorrhizal fungi, including arbuscular, orchid, ericoid and ectomycorrhizal fungi, which occur in roots and enhance plant nutrient uptake, and endophytes, which occur in roots or aboveground tissue and enhance plant defence, growth and stress tolerance
Native species	A species that has originated/evolved in a given area or arrived there without human involvement from an area where it is native (Pyšek <i>et al.</i> , 2004)
Naturalized species	An alien species that has established a self-replacing population in its new environment (Pyšek <i>et al.</i> , 2004)
Pathogen	An organism that can or does cause disease in its host. Here, we use the term to indicate a fungal or oomycete species that frequently causes disease in plants, regardless of whether it can sometimes occur in a commensal or saprotrophic state (see also Stergiopoulos & Gordon, 2014)
Specificity	The degree to which a symbiosis is restricted to a subset of a community. Where a species occurs with close phylogenetic relatives, effective specificity may be lower than for the same species occurring in the context of less closely related species
Symbiosis	Where two organisms interact in a biologically intimate, physiologically integrated association. Includes positive (mutualism), neutral (commensal), and negative (parasitic/pathogenic) interactions (De Bary, 1879)

fungus linkages on preinvasion risks, invasion trajectories, post-invasion impacts, and management options.

## II. Simplification of complex networks into interaction motifs

Plants in their native range are embedded in a network of interactions with symbiotic fungi, including pathogens and mutualists. The process of human transport and introduction of plants and fungi into new regions alters these interactions (Fig. 1) through the loss of interactions from the native range and the establishment of novel interactions between natives and aliens and between aliens from different origins. This results in many possible interaction networks involving native and alien species. The recent proliferation of hypotheses addressing biotic interactions in invasion reflects this complexity. For example, Mitchell *et al.* (2006) identify 20 and Catford *et al.* (2009) 23 different invasion hypotheses involving biological interactions.

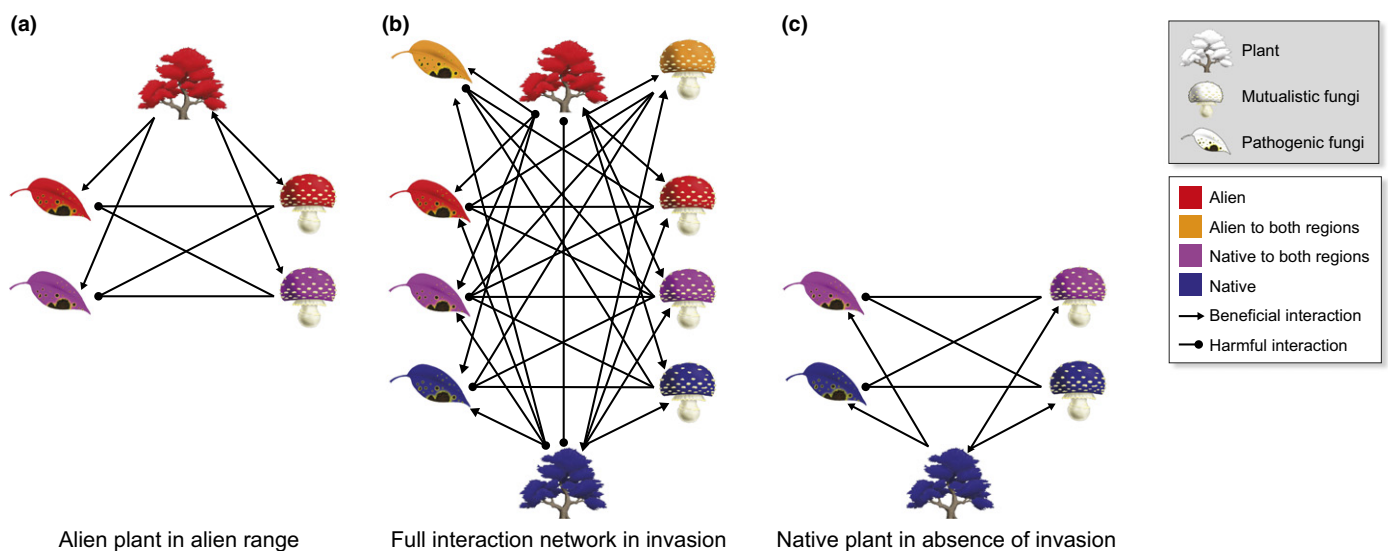
Here, we propose that these many possible plant–fungus interaction scenarios can be described by a reduced number of interaction motifs (Tables 2, 3; Stouffer *et al.*, 2007). Use of the motif approach, adopted from network theory, provides a useful tool to sort ecological hypotheses and to identify hypothetical interactions even where evidence is currently lacking (Poisot *et al.*, 2016). We first discuss the possible two-node motifs, based on the native or alien status of plant and fungus (Table 2), and then more complex three-node and higher motifs (Table 3). Each motif is summarized in the table, with evidence for and against the importance of these motifs discussed in the following sections. Even though mutualists and pathogens are often studied separately, most interaction motifs involving either mutualists or pathogens show strong similarities. Therefore, we discuss both beneficial and harmful symbioses simultaneously for each motif.

Defining interaction motifs hinges on understanding species concepts and whether those species are native or alien to a given region. This can be difficult to determine for fungi (Box 1), especially for epiphytic and endophytic fungi (Shipunov *et al.*, 2008), hence investigation into the potential role of these fungal communities in invasion has just begun (Aschehoug *et al.*, 2012; Nuñez *et al.*, 2015; Cleary *et al.*, 2016). Nonetheless, there are sufficient cases where fungal species can be defined and identified as alien to allow meaningful discussion and progress.

### 1. Reduced symbionts

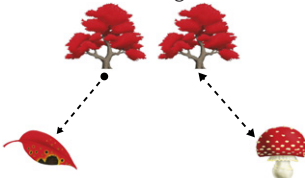
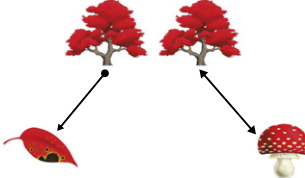
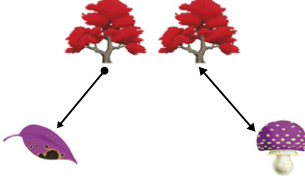
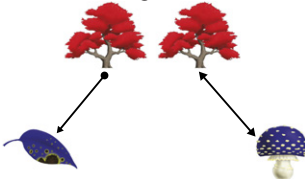
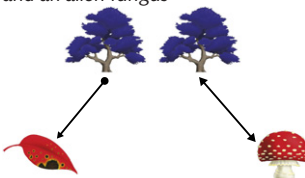
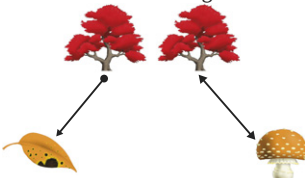
One of the most widely recognized motifs is reduced symbionts, the disruption in a plant's native fungal associations that can occur when a plant is introduced. Some fungi may not survive co-transportation or may not survive in the new environment. Furthermore, if relatively few individual plants are introduced, the bottleneck can create strong founder effects in associated fungal symbiont populations (Hayward *et al.*, 2015b). This loss of symbiont diversity may lead to *mutualism limitation* or *missed mutualists* for beneficial symbioses and *enemy release* or *enemy reduction* for antagonists (Catford *et al.*, 2009). A lack of compatible mutualists may cause the failure of plant establishment (Zenni & Nuñez, 2013), as in the failure of early efforts to establish pine plantations in the Southern Hemisphere (Richardson *et al.*, 2000).

Alternatively, a species may be inherently nonmycorrhizal (e.g. species of the Brassicaceae or Proteaceae) or may evolve to be less dependent on mycorrhizal associations in its new range (Seifert *et al.*, 2009), which could increase invasion success in disturbed environments (Richardson *et al.*, 2000; Traveset & Richardson, 2014). While some individual studies support the hypothesis of nonmycorrhizal plants being more invasive, a meta-analysis of 67 studies including a wide range of herbaceous and woody plants by



**Fig. 1** Plant–fungus interactions of (a) alien plants in their alien range and (c) native plants in the native range can include local and widespread pathogens and mutualists. Following introduction of aliens to a new range, the complexity of possible plant–fungus interactions becomes overwhelming and almost visually indecipherable, when all possible interactions of alien and native plants and fungi are considered (b). One way to unravel this complexity is to focus on two-node and higher node interaction motifs within the broader context of the full interaction network (Tables 2, 3). Drawings by S. Tourtellot.

**Table 2** Two-node interaction motifs extracted from the full complexity of interactions in Fig. 1, showing parallel motifs in pathogens and mutualists and giving explicit contrasts and comparisons. Evidence for individual motifs and examples are discussed in the text

Motif <sup>1</sup>	Pathogen mechanisms	Mutualist mechanisms	Pathogen/mutualist comparison
<p><b>Reduced symbionts:</b> alien plant in an introduced range has fewer symbionts than in its native range</p> 	<p><b>Enemy release and enemy reduction</b> where reduction in co-evolved pathogens from the native range increases invasiveness (Catford <i>et al.</i>, 2009)</p>	<p><b>Mutualist limitation or missed mutualists</b> (Catford <i>et al.</i>, 2009) where a lack of symbionts limits invasion. May be avoided by <b>reduced dependence</b>, either inherent or evolved in the novel range</p>	<p>Higher specificity of pathogens than mutualists makes enemy release potentially more common than mutualist limitation. Evidence for both remains equivocal, particularly for effects on fitness. Both are hypothesized to lead to evolutionary change</p>
<p><b>Co-introduction and co-invasion:</b> introduction of alien symbionts with alien plant, either concurrently or asynchronously</p> 	<p><b>Co-introduction and co-invasion</b> of pathogens may prevent or reduce plant invasion but can promote invasion via spillover (see Table 3). Introduction of pathogens from alien range for biological control represents deliberate, asynchronous co-introduction</p>	<p><b>Co-introduction and co-invasion</b> of alien mutualists can prevent mutualist limitation (Dickie <i>et al.</i>, 2010). Commonly reported in invasive ectomycorrhizal trees; less so in other mutualisms. Includes intentional co-introduction of mutualists to enhance growth</p>	<p>Co-introduction and co-invasion appear common for both pathogens and mutualists, particularly for highly specific associations, and have well-documented ecological effects. High frequency of co-invasion may reflect a sampling bias towards successful invasions and obvious pathogens</p>
<p><b>Familiar associations:</b> alien plant or fungus encounters a symbiont species native to both its native and alien ranges</p> 	<p><b>Familiar pathogens</b> may prevent enemy escape and thus limit plant invasion. Few familiar pathogens have been documented, reflecting true endemism or lack of knowledge of native ranges (Box 1)</p>	<p><b>Familiar mutualisms</b> prevent mutualist limitation and may facilitate faster spread if mutualists are already widespread in the environment. Common for many invasive plants, particularly arbuscular mycorrhizas</p>	<p>Familiar mutualists appear common and familiar pathogens rare, maybe reflecting faster speciation rates associated with parasitism (Chaverri &amp; Samuels, 2013). In both cases, defining fungal species and geographical ranges is critical to determining whether a fungus is 'familiar' or not (Box 1)</p>
<p><b>Novel associations</b> between an alien plant and a native fungus</p> 	<p><b>Novel pathogens</b> of alien plants contribute to <b>biotic resistance</b> and <b>enemy accumulation</b> through either a broad host range or genetic adaptation to novel hosts (van der Putten, 2010). May be underreported if leading to establishment failure</p>	<p><b>Novel mutualisms</b> appear fairly common and may prevent mutualist limitation. May lead to <b>enhanced mutualisms</b> if the alien plant receives disproportionate benefit (Callaway <i>et al.</i>, 2004)</p>	<p>Both rely on low host specificity of fungi, or the ability of fungi to host switch through adaptation. Relative importance of genetic adaptation remains unclear</p>
<p><b>Novel associations</b> between a native plant and an alien fungus</p> 	<p><b>Novel pathogen associations</b> with native plants are the cause of many emerging diseases which can drive major ecosystem diebacks</p>	<p><b>Novel mutualist associations</b> are most frequently recorded for well-known fungi and fungi with large economic effects (Dickie <i>et al.</i>, 2016). Effects of alien fungi on native plants remain largely unknown</p>	<p>Strongly disproportionate reporting, with alien fungi commonly reported as pathogens of native plants, but few examples of alien mutualists on native plants. This may partially reflect a bias assuming new pathogens are alien, but newly described mutualists are not</p>
<p><b>Co-xenic novel associations:</b> plant and fungal symbionts are both alien in the introduced range but do not naturally co-occur in their native ranges</p> 	<p><b>Co-xenic novel pathogens</b> may reduce plant invasiveness. Generalist pathogens with a broad host range are most likely to form co-xenic associations</p>	<p><b>Co-xenic novel mutualisms</b> may prevent mutualist limitation and should be most common where symbionts are generalists</p>	<p>Both require a broad host-range fungus not already present as a native. May be more commonly described in pathogens than mutualists</p>

<sup>1</sup>See Fig. 1 for a full explanation of colours, icons, and arrow types. Dashed lines indicate a broken or disrupted linkage.



Bunn *et al.* (2015) found that arbuscular-mycorrhizal colonization of invasive plants is no lower than colonization of native species across studies. Similarly, Menzel *et al.* (2017) found that nonmycorrhizal alien species are not more widely spread than obligate mycorrhizal alien species in Europe. Menzel *et al.* (2017) suggested that facultative mycorrhizal species may actually be more widely spread than either obligate arbuscular or nonmycorrhizal plants, but the analysis of facultative species has to be treated with caution as more frequently observed species are more likely to be classified as facultative in their database (at the extreme, a species with only one observation of presence or absence of mycorrhizas cannot be considered facultative in that analysis; T. Kuyper, pers. comm.).

In contrast to the loss of mutualists, loss of pathogens (a component of enemy release) may increase plant fitness and promote invasion. Plant species are often infected by fewer pathogens in their introduced than in their native range (Jeschke, 2014), particularly for plant pathogenic fungi (Mitchell & Power, 2003). This includes, for example, planted rubber trees in Asia which have escaped *Microcyclus ulei*, the cause of South American leaf blight (Desprez-Loustau *et al.*, 2007), or reduced pathogen load on *Eucalyptus* outside of Australia (Wingfield *et al.*, 2008). However, there is much less empirical evidence that pathogen release provides a competitive advantage to invasive plants or determines invasion success (Parker & Gilbert, 2007; Heger & Jeschke, 2014; Blackburn & Ewen, 2016). In particular, studies frequently fail to find lower levels of pathogen attack on aliens compared with native species within the same location (Colautti *et al.*, 2004; Vacher *et al.*, 2010). Overall, Heger & Jeschke (2014) found that only 33% of studies actually support the enemy release mechanism. Even where an initial advantage from enemy release does occur, this may diminish over time (Diez *et al.*, 2010; Flory & Clay, 2013), driven by co-invasion of pathogens and novel associations with native pathogens (discussed in next section), including fungal adaptation to novel hosts.

Taken as a whole, the evidence for a general pattern of decreased or increased invasiveness following mutualist limitation or enemy release remains equivocal. This suggests that maintenance or re-establishment of fungal symbioses is common in plant invasions. Thus, the ways in which plant–fungal associations are maintained or re-established, as described in the following motifs, are critical to understand in order to better predict invasion dynamics.

## 2. Mechanisms of maintaining symbioses

Given that many alien plants do not show reduced symbionts in the introduced range, a key question becomes how these interactions can be maintained. This can occur through co-introduction and co-invasion, or when symbionts from the alien range are already present as natives in the introduced range (Dickie *et al.*, 2010; Nuñez & Dickie, 2014).

*Co-introduced associations* occur where alien plants interact with fungi from their native range that are not native to the introduced range. Simultaneous introduction can occur when plants are transported with soil, or through transport of plants or propagules with systemic infections, as occurs for endophytes with vertical transmission (Rudgers *et al.*, 2005; Shipunov *et al.*, 2008).

Reassociation of plants and fungi introduced at different times can also lead to co-introduced symbionts. Co-introduced symbionts can enhance plant invasiveness, resulting in increased probability of *co-invasion*, where both plant and fungus become invasive. This has largely been documented for co-invasion of ectomycorrhizal pines with their native fungal symbionts in the Southern Hemisphere (Dickie *et al.*, 2010; Hayward *et al.*, 2015a), but endophytic fungi in aboveground tissue can also enhance the invasion success of grasses and forbs (Rudgers *et al.*, 2005; Shipunov *et al.*, 2008). Co-invading mutualists are likely to be a subset of the normal range of associated fungi, and may not maintain the same level of host benefit. For example, Moeller *et al.* (2016) found that *Pseudotsuga* invading grasslands showed nutrient deficiency, despite adequate mycorrhization with co-invasive fungi, suggesting that co-invading mutualists may have been less beneficial than fungal associates found in plantations or native forest. A more extreme example occurs where mutualists provide defence against enemies not present in the invasive range. For example, fungi in the genus *Epichloë* are mutualistic foliar endophytes of *Brachypodium sylvaticum* in the native range, but no longer provide a benefit to the host in the introduced range. Thus, co-invasion of plant and fungus results in a negative interaction, rather than the positive association seen in the native range (Vandegrift *et al.*, 2015).

Co-introductions are well documented for alien pathogenic fungi, which are most often introduced as contaminants of imported commodities or plant material (Hulme *et al.*, 2008). Co-introductions of pathogens with plants have a direct negative effect on the host plant. Hence, while co-invasion of pathogens and plants is possible, the effect of pathogens is often to reduce the fitness and/or local abundance of invasive plants (Diez *et al.*, 2010). Multiple asynchronous co-introductions can lead to pathogen accumulation over time, reducing any advantage of enemy release. This may have occurred for *Eucalyptus* spp. in many countries where they have been introduced (Wingfield *et al.*, 2008). Deliberate co-introduction of native pathogens is used as biocontrol of alien plant species, including, for example, the release of European blackberry-rust fungus, *Phragmidium violaceum*, as a biocontrol agent in Australia (Morin & Evans, 2012). Co-introduction is also an important means of introduction for alien pathogens that then form novel associations with native plants (discussed in Section 3).

*Familiar associations*, where symbionts from the native range of an organism are already present in the invasive range, may also prevent reduced symbionts following introduction. For example, it has been suggested that arbuscular mycorrhizas have a low level of endemism (Davison *et al.*, 2015) and low specificity (but see Box 1), and so are ‘familiar’ to alien hosts (Richardson *et al.*, 2000). The same has been suggested for some widespread ectomycorrhizal fungi and endophytes (e.g. *Cenococcum geophilum* and *Phialocephala fortinii* on invasive *Pinus contorta* in New Zealand; Dickie *et al.*, 2010). We note that Dickie *et al.* (2010) referred to these as ‘cosmopolitan associations’, but we suggest a better term is ‘familiar associations’ as a fungus may be ‘familiar’ (i.e. native to both regions) without being truly cosmopolitan (i.e. present around the world; see Box 1).

Within pathogens, familiar associations are less well documented. This may reflect fast speciation rates associated with

**Table 3** Three-node and higher interaction motifs; most three- and higher node motifs follow from one or more two-node motifs (Table 2)

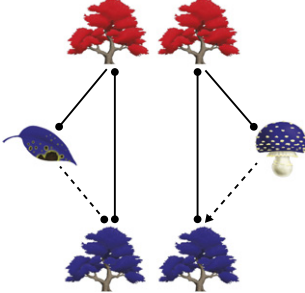
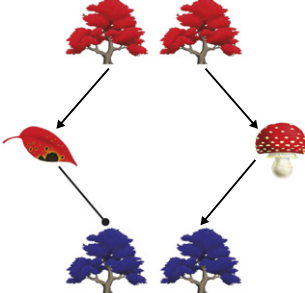
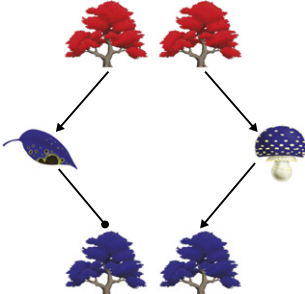
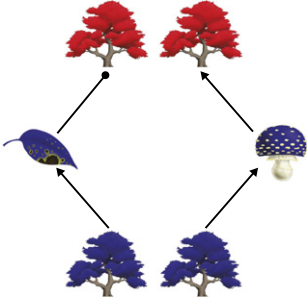
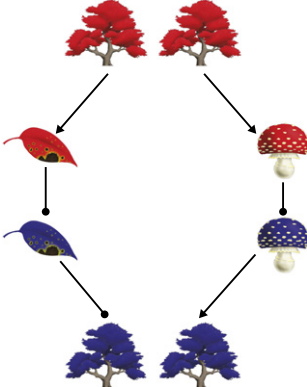
Motif <sup>1</sup>	Pathogen mechanisms	Mutualist mechanisms	Pathogen/mutualist comparison
<p><b>Symbiont disruption</b> (follows from <b>reduced symbionts</b>). Alien plants disrupt the association between a fungus and a native plant, either directly by reducing fungal abundance, or indirectly by reducing host plant abundance</p> 	<p><b>Pathogen disruption</b> is a hypothetical corollary to mutualism disruption, caused either directly or indirectly. Some invasive plants may suppress pathogens (Zhang <i>et al.</i>, 2009) but the effect on plant invasion dynamics remains unclear</p>	<p><b>Mutualism disruption</b>, where plants without a particular mutualist disrupt or reduce abundance of mutualists on other plants through direct antagonism towards the mutualist or indirectly by competitive reduction of host plants (both mechanisms shown; Stinson <i>et al.</i>, 2006)</p>	<p>Currently only documented for mutualists. Suggested for pathogens, but rigorous evidence is lacking</p>
<p><b>Symbiont spillover</b> (follows from <b>co-invasion</b>). Local population of alien plant drives interaction of alien fungus with native host</p> 	<p><b>Pathogen spillover</b> of alien pathogens from alien plants onto co-occurring native plants can enhance invasion and increase invasion impacts. Part of the <b>enemy of my enemy</b> or <b>disease-mediated invasion</b> hypothesis. Can result in <b>apparent competition</b></p>	<p><b>Mutualist spillover</b> occurs when mutualists of invasive plants also associate with native plants. Novel associations of alien ectomycorrhizal fungi and native plants have been documented (Table 2), but not linked to local populations of invasive plant. Would lead to <b>apparent facilitation</b></p>	<p>Currently only documented for pathogens. The presence of novel mycorrhizal associations near alien host plants suggests mutualist spillover does occur, but the dynamics and impacts have not been characterized</p>
<p><b>Symbiont spillback</b> (follows from <b>novel associations</b> and/or <b>familiar associations</b>). Alien plant increases local population of native fungi, with impact on native plant–fungal interaction</p> 	<p><b>Pathogen spillback</b> where native pathogen abundances increase on alien hosts, increasing colonization of co-occurring native plants. Part of the <b>enemy of my enemy</b> or <b>disease-mediated invasion</b> hypothesis. Can result in <b>apparent competition</b></p>	<p><b>Mutualist spillback</b> is a hypothetical pair with pathogen spillback, which would occur if alien plants support native fungal mutualists and hence facilitate native plant associations. Would lead to <b>apparent facilitation</b></p>	<p>Currently only documented for pathogens. Distinguishing spillover from spillback requires knowledge of fungal origins, which may not be possible (Box 1)</p>

Table 3 (Continued)

Motif <sup>1</sup>	Pathogen mechanisms	Mutualist mechanisms	Pathogen/mutualist comparison
<p><b>Subsidized symbiosis</b> (follows from <b>novel associations</b>, <b>familiar associations</b>, or <b>co-invasion</b>). Native plant increases local population of native or alien fungi, with impact on alien plant–fungal interaction</p> 	<p><b>Subsidized pathogen</b> occurs where native plant populations support pathogens that attack alien plants. Similar to <b>pathogen spillback</b>, except native, rather than alien, plants experience a net benefit. May contribute to <b>biotic resistance</b></p>	<p><b>Subsidized mutualism</b> occurs where native plants facilitate alien plants by supporting mutualists more beneficial to the alien than to themselves (Bever, 2002)</p>	<p>Subsidized symbiosis may occur with native (shown) or alien fungal symbionts (not shown). Similar to spillover and spillback, but fungal abundance is driven by native, not alien, plant populations. May occur through the population dynamics of fungi or, at least in the case of mycorrhizal fungi, through an imbalance of trade and/or resource transfer through mycorrhizal networks</p>
<p><b>Symbiont displacement</b> (follows from <b>co-invasion</b> and <b>spillover</b>). Alien fungal symbiont competitively displaces native fungal symbiont</p> 	<p><b>Pathogen displacement</b> as a consequence of competition between fungi for hosts could lead to the replacement of native pathogens by alien pathogens</p>	<p><b>Mutualist displacement</b> is competitive displacement of native fungi by alien mutualists. Supported by evidence of competition among fungi, but not yet fully demonstrated</p>	<p>Although competition is often invoked as a mechanism for plant biodiversity loss in invasion, competitive displacement of fungi has not been demonstrated for either invasive pathogens or mutualist fungi. Competition may occur for either plant host resources or soil resources</p>

<sup>1</sup>See Fig. 1 for a full explanation of colours, icons, and arrow types. Dashed lines indicate a broken or disrupted linkage.

parasitism (Chaverri & Samuels, 2013), or, alternatively, familiar associations may be under-recognized, either because they contribute to invasion failure (Zenni & Nuñez, 2013) or because species boundaries and native ranges are not understood (Box 1). Notwithstanding this, some examples include the widespread pathogen *Alternaria brassicicola*, which attacks, and may limit the invasion success of, the littoral plant *Cakile maritima* in many nonnative ranges (Thrall *et al.*, 2001).

### 3. Mechanisms of establishing new symbioses

An alternative to maintaining symbioses is to form new ones. Organisms arriving in a new area encounter novel potential symbionts.

*Novel associations* occur where an alien plant or fungus interacts with symbionts not found in its native range. The extent of novel associations may be influenced by the degree of phylogenetic relatedness between the invasive plant and resident species in the area of introduction (Vacher *et al.*, 2010; Bufford *et al.*, 2016), as phylogenetically close species tend to share more pathogens (Parker *et al.*, 2015; Gilbert & Parker, 2016) and, potentially, mutualists.

Novel associations have been well documented in some ectomycorrhizal trees, with native fungi forming either the majority (e.g. planted *Eucalyptus* in the Seychelles; Tedersoo *et al.*, 2007; planted *Pinus* in Iran; Bahram *et al.*, 2013) or a portion of associations on alien plants (e.g. invasive *Pseudotsuga* in New Zealand; Moeller *et al.*, 2015). A mixture of novel associations and co-invasion has also been found for foliar endophytes (Shipunov

**Box 1** Identifying fungi and their native ranges remains a challenge

Invasive species management depends on identifying species and native ranges. Fungi encompass several million species but most are undescribed (Taylor *et al.*, 2014). Even where species are known, limited historical records hinder identification of what is native or alien (e.g. Pringle & Vellinga, 2006). Indeed, fungi are often first described or only known from an invasive range (e.g. ectomycorrhizal *Rhizoglyphus*; Galan & Moreno, 1998; pathogenic *Phytophthora ramorum*; Brasier, 2001; Grünwald *et al.*, 2012). It is likely that most invasive fungi remain undetected, with a bias towards detecting pathogens, and brightly coloured and poisonous species (Dickie *et al.*, 2016).

Species concepts in fungi are often unclear, making identification and range mapping more difficult. Genetic approaches have helped, but controversies remain. For example, the fungi that form arbuscular mycorrhizal mutualisms are considered cosmopolitan species by some authors (Davison *et al.*, 2015); this depends on the level of variability in the gene region used to define species (Brunns & Taylor, 2016).

Baseline data on native fungi are essential to disentangle new invasions from environmentally triggered population changes (including pathogen outbreaks). Recently published global surveys targeting mycorrhizal fungi (Kivlin *et al.*, 2011; Davison *et al.*, 2015) and forest soil fungi (Tedersoo *et al.*, 2014) and website compilations (e.g. [www.mushroomobserver.org](http://www.mushroomobserver.org), [www.inaturalist.org](http://www.inaturalist.org) and [www.gbif.org](http://www.gbif.org)) are helpful steps forward. Aggregating existing data into a single database, standardizing methods, and improving metadata will provide essential knowledge of species identities and distributions and facilitate synthesis.

*et al.*, 2008). Novel associations of alien plants with native pathogens have also been reported, including *Armillaria novae-zealandiae* on *Pinus radiata* in New Zealand (Hood *et al.*, 2008), *Collybia fusipes* on *Quercus rubra* in France (Piou & Seastedt, 2002), and *Pyrenophora semeniperda* and *Ustilago* spp. on invasive *Bromus tectorum* in North America (Mordecai, 2013a; Prev y *et al.*, 2015). These novel associations between native pathogens and alien plants may drive *biotic resistance*, where negative interactions with the recipient pathogen community prevent invasion (Levine *et al.*, 2004). While novel interactions between alien plants and native pathogens clearly do occur, documented cases of invasion failure caused by these novel interactions are limited (Flory & Clay, 2013) or are context specific (Mordecai, 2013a). This may reflect the effectiveness of biotic resistance in preventing initial establishment, creating a potential reporting bias. Some evidence for biotic resistance is present in the effects of native pathogenic fungi on the success of alien forestry species (e.g. *Heterobasidion annosum* on *Picea sitchensis* in the UK; *Puccinia psidii* on *Eucalyptus* in South America; *Chrysosporthe* species causing canker on *Eucalyptus* in multiple countries; *Gremmeniella abietina* on *P. contorta* in Sweden) and crops (e.g. *Mycena citricolor*, the agent of American leaf spot of coffee on *Coffea arabica*; *Fusarium oxysporum* on cotton, *Gossypium hirsutum*, in Australia; Wang *et al.*, 2010).

Novel associations also occur when introduced fungi associate with native plants. These have been described for European ectomycorrhizal fungi (*Amanita* spp.) in North America, New

Zealand and Argentina, Australian ectomycorrhizal fungi (*Laccaria*) in Spain, and a few other species (Diez, 2005; Wolfe & Pringle, 2012; Dickie *et al.*, 2016; Berch *et al.*, 2017). Novel associations of alien pathogens with native plants are a main cause of emerging plant diseases (Anderson *et al.*, 2004; Parker & Gilbert, 2004; Desprez-Loustau *et al.*, 2007), especially in forests (Santini *et al.*, 2013). Prominent examples include sudden oak death (Gr nwald *et al.*, 2012) and myrtle rust (Carnegie *et al.*, 2016). Most novel associations occur following co-introduction with alien plants. Liebhold *et al.* (2012) estimated that nearly 70% of damaging forest insects and pathogens established in the USA between 1860 and 2006 probably entered on imported live plants and this is still considered a major pathway of pathogen introductions (Jung *et al.*, 2015). A classic example is *Cryphonectria parasitica*, the agent of chestnut blight, which devastated north-eastern US forests in the early 20<sup>th</sup> Century and was probably introduced with *Castanea crenata* from Asia (Anagnostakis, 1987). Alien fungi are also introduced on timber or other plant-derived materials. The devastating pandemics of Dutch elm disease probably resulted from imports of elm, *Ulmus*, timber infested with *Ophiostoma ulmi* and *O. novo-ulmi* (Brasier, 2001).

Global movement of plants and fungal pathogens has increased the probability that plants and fungi native to different regions of the world will encounter each other in a common introduced range, potentially establishing *co-xenic* ('with foreigner') *novel associations* (Nu ez & Dickie, 2014). This term was coined to describe the observed association of *Eucalyptus* from Australia with ectomycorrhizal *Amanita muscaria* from Europe in New Zealand (Nu ez & Dickie, 2014), but is common in pathogens. For example, the oomycete *Phytophthora cinnamomi*, presumed native to southern Asia and noted as a pathogen on >3000 host species world-wide, has been introduced into many temperate and subtropical regions, where it has established novel associations with many plant species, both native and alien, in primary production, ornamental plantings and natural ecosystems, for example with *Q. rubra* in France (Delatour, 1986).

#### 4. Increasing complexity: three-node and higher motifs

Each of the two-node interaction motifs described in Table 2 are embedded in ecological communities and thus must be understood within a broader context to fully appreciate the impacts of invasion. There are, however, interactions that *necessarily* require simultaneous consideration of three or more nodes (Table 3). Given the 10 nodes identified in Fig. 1, there are many (>30) possible three-node and higher interaction motifs. We focus on the subset of those higher order motifs for which we have clear evidence for their ecological importance. Each higher order motif follows naturally from particular two-node motifs.

One example of this is *symbiont disruption*, which has been demonstrated where a nonmycorrhizal alien plant suppresses symbioses of native plants (Stinson *et al.*, 2006; Meinhardt & Gehring, 2012). This may occur either if the alien plant supplies fewer resources to mutualists (Vogelsang & Bever, 2009), resulting in lower mutualist availability, or, as in the Brassicaceae, through active production of inhibitory compounds by the plant (Stinson *et al.*, 2006). Both arbuscular mycorrhizas and ectomycorrhizas can



be suppressed in this way, and the mechanism has been demonstrated in several cases, including brassicas (Stinson *et al.*, 2006; Wolfe *et al.*, 2008; Pakpour & Klironomos, 2015) and tamarisk, *Tamarix* sp. (Meinhardt & Gehring, 2012). A similar pattern of symbiont disruption has been suggested in the context of fungal pathogens, based on the inhibition of *Pythium* and *Rhizoctonia* by root exudates of invasive *Solidago* (Zhang *et al.*, 2009); however, further work is needed to show that the exudate concentrations used in these assays are realistic for field soils.

Similarly, the two-node motif co-invasion can lead to *symbiont spillover*, where co-invasive alien fungi become abundant on their alien plant host and consequently spread onto native hosts. Symbiont spillover has most frequently been discussed in the context of pathogens. Although co-introduction and subsequent novel associations of alien fungi on native hosts are well documented, only a few examples of true spillover driven by population growth of invasive plants have been described so far. The key distinction is that 'spillover', as originally defined in the context of invasions (Power & Mitchell, 2004), requires that the pathogen dynamics be primarily driven by transmission from an alien host, rather than transmission within the native host population. One example is the role of *Rhododendron ponticum* as an invasive alien reservoir host for *Phytophthora ramorum* and *Phytophthora kernoviae* in Scotland (Purse *et al.*, 2013). Spillover has also been observed in the co-xenic novel association of the invasive tree *Syzygium jambos*, which originates from southeast Asia, and guava rust, *Puccinia psidii*, from Brazil. The resulting increased inoculum pressure on native Myrtaceae has been detrimental in both Hawaii and Australia (Carnegie *et al.*, 2016). There may be corollaries to pathogen spillover in mutualisms as, for example, ectomycorrhizal fungi have been shown to spread from alien trees onto neighbouring natives (Diez, 2005; Berch *et al.*, 2017), but the consequences for native plant fitness remain unknown.

*Symbiont spillback* is a similar process to spillover, except that it involves native fungi which increase in abundance as a consequence of novel associations with invasive host species, resulting in an increasing, typically adverse, effect on native species (Strauss *et al.*, 2012). Both pathogen spillover and spillback, which may be difficult to distinguish, are encompassed in the *enemy of my enemy hypothesis* (Colautti *et al.*, 2004) or *disease-mediated invasion hypothesis* (Strauss *et al.*, 2012) and have been supported by empirical work (Flory & Clay, 2013). Siam weed (*Chromolaena odorata*) from North America, for example, accumulates *Fusarium* spp. soil pathogens which inhibit the growth of surrounding native plants (Mangla *et al.*, 2008). Day *et al.* (2016) showed that the highly invasive *Vincetoxicum rossicum* benefits from associating with soil microbes that increase its growth but are pathogenic on native plants. Similarly, the alien cheatgrass (*Bromus tectorum*) is a reservoir species for the naturally occurring seed pathogen *Pyrenophora semeniperda* which was then able to attack native grasses in western North America (Beckstead *et al.*, 2010). However, in this case, the shared pathogen actually promotes native and alien grass co-existence by reducing alien plant dominance (Mordecai, 2013b). Spillback has been sparsely investigated in mutualisms, but Dickie *et al.* (2014) found no evidence of increased ectomycorrhizal colonization of native shrubs in soils from under alien *P. contorta*.

Other three-node and higher interaction motifs could be proposed and tested, but the above encompass the best empirically documented motifs. Heretofore unexplored motifs could prove important in the future. For example, there is evidence of *subsidized mutualism*, where native plants support fungal populations that give disproportionate benefits to alien hosts (Callaway *et al.*, 2001; Bever, 2002). As an example of a more complex four-node interaction, invasive fungi may competitively displace native fungi of either the same functional type or of other mycorrhizal types (Kohout *et al.*, 2011), suggesting *symbiont displacement*. For example, there is evidence that valuable truffle fungi in plantations may be displaced by less valued species (Murat *et al.*, 2008). Finally, none of the earlier hypotheses specifically address interactions between mutualists and pathogens (e.g. competition for host resources). Recent work is beginning to explore some of these possible scenarios (Sillo *et al.*, 2015), but the ecosystem effects of these higher order interactions remain largely untested in the context of invasion.

### III. Plant–fungal interactions and plant invasion dynamics

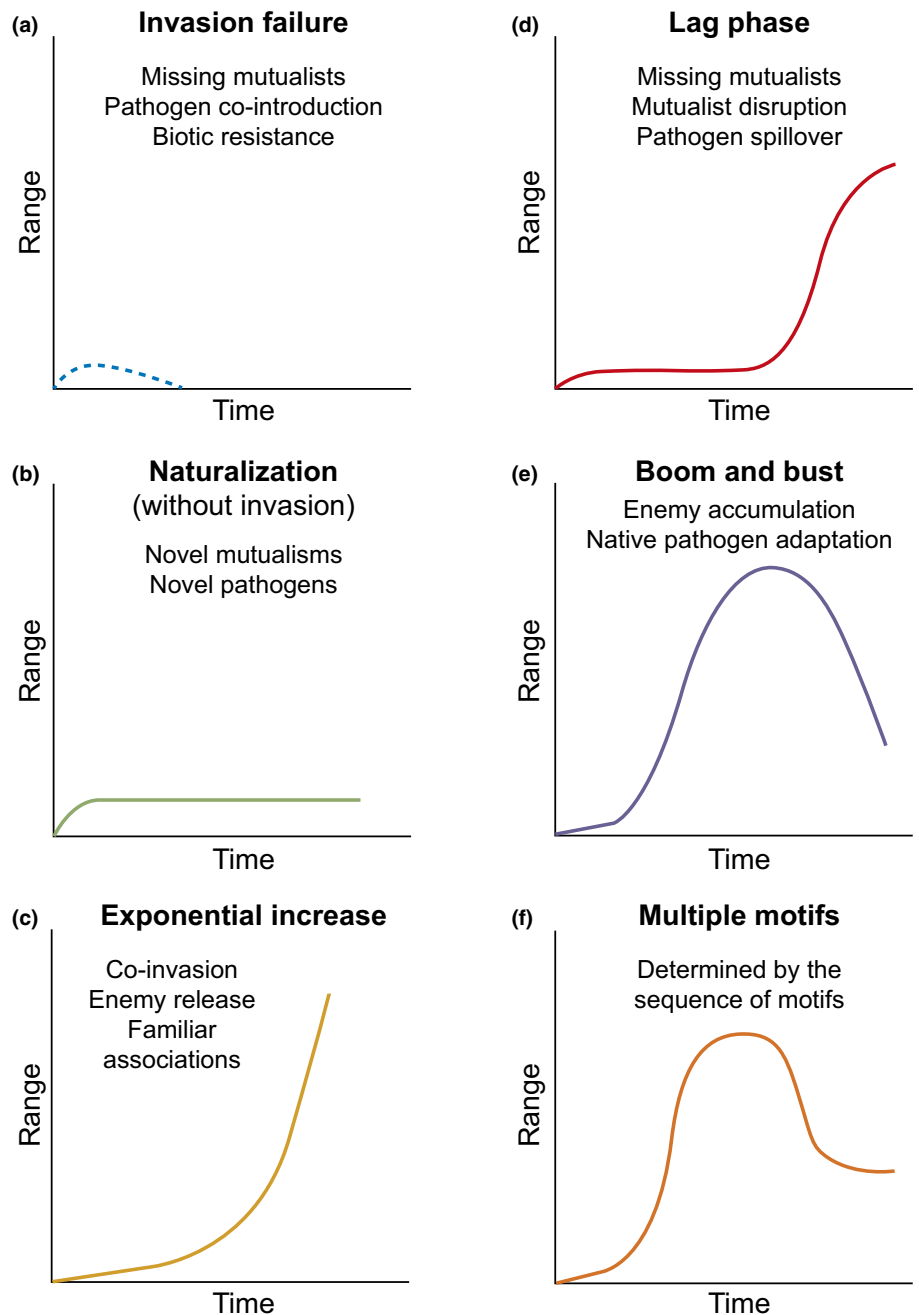
While interactions with symbiotic fungi are known to impact alien plant performance, linking these effects to the population growth of aliens has been far less frequently explored. Populations of alien species can undergo complex trajectories, including invasion failure (Diez *et al.*, 2009), extended lag phases (Crooks, 2011), exponential growth, and boom-and-bust cycles (Simberloff & Gibbons, 2004). Plant–fungal interactions have the potential to play a role in all these trajectories (Fig. 2). Invasion failure (Fig. 2a), for example, remains poorly understood (Diez *et al.*, 2009; Zenni & Nuñez, 2013), but reduced mutualisms may limit Pinaceae invasions (Richardson *et al.*, 2000; Nuñez *et al.*, 2009; Pringle *et al.*, 2009). Biotic resistance, where native pathogens form novel associations with introduced plants, may also lead to the failure of some introductions (Dinoor & Eshed, 1984; Levine *et al.*, 2004). A meta-analysis by Levine *et al.* (2004) suggests that fungi have strong but contrasting effects on the performance of alien seedlings. Glasshouse studies using sterilized soil have shown evidence of biotic resistance driven by pathogens (Beckstead & Parker, 2003; Knevel *et al.*, 2004), but these effects are often smaller than the positive effects of mutualists (Reinhart *et al.*, 2003). Either the presence of pathogens or the absence of mutualists may not be sufficient to prevent establishment but may reduce the rate of population growth and abundance so the alien plant species establishes and becomes naturalized but never becomes invasive, or its invasion remains limited (Levine *et al.*, 2004; Fig. 2b). Alternatively, escape from pathogens can allow alien plants to increase dramatically in both range and abundance, especially if not impeded by a dependence on specific mutualists (Fig. 2c).

Where the failure of species to become invasive reflects mutualist limitation, the subsequent arrival of mutualists may relieve that limitation. It has been suggested that this can lead to 'lag phase' invasions (Fig. 2d), where a species is present for an extended period and then becomes more invasive (Diez, 2005;

Hallett, 2006). In some cases, deliberate introduction of mutualist fungi to enhance productivity may greatly enhance the invasiveness of plants that were previously not problematic (e.g. *Pseudotsuga menziesii* in New Zealand following the deliberate addition of *Rhizopogon parksii* to forest nurseries). By contrast, soil feedbacks over time may become more negative (Diez *et al.*, 2010), resulting in boom-and-bust dynamics of alien plants (Fig. 2e) or long-term monotonic decline (not shown), although the degree to which this is driven by population increases, adaptation of native or alien pathogens to novel hosts, or negative feedback within mutualisms (Bever, 2002) remains unclear. Many of these interactions can occur in parallel or consecutively, potentially leading to complex trajectories (Fig. 2f).

#### IV. Predicting where plant–fungal interactions matter: plant–symbiont specificity, dependence and effect size

The specificity, dependence and effect size of the interaction, including both the direction and magnitude of the effect, are major determinants of the extent to which a given plant–fungal association matters in invasion. In particular, the degree of interaction specificity and the effect of fungi on plant growth provide useful guidance as to which interactions lead to which motifs (Table 4). The abiotic environment is also likely to play a major role in determining when and where plant–fungal interactions have their greatest effects.



**Fig. 2** Theoretical plots of plant invasion (range expansion) over time depicting dynamics that could be explained by linked plant–fungal invasions. Although framed from a plant perspective, in principle similar patterns should occur for fungal symbiont populations. Processes may occur consecutively or in parallel, and some dynamics may be subsets of others (e.g. b, d; c, e).

## 1. Symbiosis specificity

Host specificity has important implications for linked plant–fungal invasions. Specificity is complex, depending on both phylogenetic distance and environmental context. A fungus might be, for example, effectively specific to an alien pine tree in the context of invasion into grasslands with no established ectomycorrhizal plants, but show no specificity in the context of invasion into a forest with established congeneric trees. Highly specific plant–mycorrhizal associations are more likely to result in mutualist limitation, thus decreasing plant or fungal invasion. High symbiont specificity may, for example, explain the relative paucity of orchid invasion, as orchids have highly specific and highly dependent mycorrhizal associations (Pyšek, 1998). Orchids comprise 9% of plant diversity, but are infrequent as invasive weeds (e.g. 0.1% of invasive terrestrial plants in the European Invasive Alien Species Gateway; 0.5% of the Global Compendium of Weeds, 2012). The few orchids that are invasive have atypically broad symbiont specificity (Bonnardeaux *et al.*, 2007; De Long *et al.*, 2013), thus being the exceptions that prove the rule. By contrast, co-introduction and co-invasion can allow some highly specific associations to invade. For example, co-invasion of ectomycorrhizal fungi with *Pinus* and *Alnus* has made them some of the most successful invasive trees in the Southern Hemisphere, despite highly specific mycorrhizal associations (Bogar *et al.*, 2015). This has resulted in a remarkably uniform invasion process across multiple invasions, with highly similar fungal communities described in *Pinus* invasions in South America (Hayward *et al.*, 2015a,b), New Zealand (Dickie *et al.*, 2010), and Hawaii (Hynson *et al.*, 2013) and a strong similarity between these invasive communities and early-successional communities within the native range (Collier & Bidartondo, 2009).

Many fungal mutualisms are not highly specific (Molina & Horton, 2015) and, for these, mutualist limitation and co-invasion are likely to be less important. The vast majority of ecosystems have arbuscular mycorrhizal associations dominated by species in the widespread order Glomerales, many of which have low host specificity, although plant–fungal community correlations have been found (Martínez-García *et al.*, 2015; Valyi *et al.*, 2015). The widespread low host specificity of arbuscular mycorrhizal fungi means that arbuscular mycorrhizal plants are less likely to show mutualism limitation or to rely on co-invasion (McGinn *et al.*, 2016), with rare exceptions where arbuscular mycorrhizal plants invade entirely ectomycorrhizal systems (Spence *et al.*, 2011).

Nonetheless, arbuscular mycorrhizal fungal communities associated with co-occurring invasive and native plants can differ substantially (Bunn *et al.*, 2015), possibly reflecting a greater reliance of alien plants on widespread generalist fungi than native plants, as suggested by a continental scale molecular survey (Moora *et al.*, 2011). Among ectomycorrhizal species, *Pseudotsuga menziesii* has relatively low specificity for ectomycorrhizal fungi, and forms at least some novel associations with native fungi when invasive (Moeller *et al.*, 2015). Similarly, several invasive fungi, including *Amanita* spp., have spread from introduced plants onto native hosts, indicating that their invasion is not limited by a lack of mutualist hosts (Wolfe & Pringle, 2012; Dickie *et al.*, 2016; Berch *et al.*, 2017).

Host specificity in plant–pathogen associations is also expected to affect plant invasion dynamics. High host specificity may increase the likelihood of enemy release, as host-specific, obligate pathogens may be less likely to be transported and achieve establishment than less specific or facultative pathogens (Mitchell & Power, 2003). Furthermore, host-specific pathogens within the recipient community are less likely to infect a novel host, leading to differential enemy pressure for native vs alien plants and enemy release for the invaders. By contrast, pathogen spillover, spillback and biotic resistance, which include novel interactions, necessarily require lower host specificity (Parker & Gilbert, 2004).

Among pathogens, low host specificity is expected to increase the invasion success of the pathogens themselves. Some generalist pathogens, especially in the genus *Phytophthora*, have successfully invaded ecosystems in several continents on very different hosts. An illustrative example is *P. ramorum*, which causes sudden oak death in northwestern America but larch disease in Europe. Similarly, *P. cinnamomi* causes dieback and mortality of many endemic species in Australia (Shearer *et al.*, 2014), but is associated with *Quercus* and *Castanea* declines in Europe (Brasier, 1996).

Although high host specificity may often prevent pathogen invasions, some pathogens with limited phylogenetic host ranges are nonetheless successful invaders (Philibert *et al.*, 2011). The apparent paradox between high host specificity and invasion success may be a result of an increased probability of pathogen establishment if it finds host plants closely related to its original host plant species (Gilbert & Webb, 2007; Saul & Jeschke, 2015; Gilbert & Parker, 2016). Adaptation leading to host shifts is also common, and again more likely to occur onto a closely related plant host (Slippers *et al.*, 2005). Heteroecious fungal pathogens, which

**Table 4** The different linked plant–fungal interaction motifs (Tables 2 and 3), mapped against the effect on the invasive plant and the degree of specificity of the interaction

		Size of effect on alien plant	
		Strong	Weak
Fungal symbiont specificity to alien plant host <sup>1</sup>	High	Reduced symbionts leading to enemy release or mutualist limitation, co-invasion, and symbiont displacement	Reduced symbionts leading to reduced dependence for mutualists
	Low	Familiar associations, novel associations, enemy accumulation, subsidized symbiosis, and symbiont accumulation	Symbiont spillover and symbiont spillback

<sup>1</sup>Specificity of a symbiont is relative to context, with, for example, the presence of established, closely related plant species reducing the effective specificity of a symbiont.

require more than one plant host to complete their life cycle, face a particularly high barrier to invasion. The invasion success of rusts (Desprez-Loustau *et al.*, 2010; Bufford *et al.*, 2016), which are often heteroecious and highly host-specific, may thus seem puzzling. In this case, other fungal traits, including high dispersal ability and ability to undergo multiple asexual cycles on alternate hosts, may reduce the importance of host specificity in limiting invasion (Philibert *et al.*, 2011). A particularly good example of this is white pine blister rust, *C. ribicola*, to which the white pine group (*Pinus* subsection *Strobus*) and a broad range of alternate hosts within the *Ribes* and *Castilleja* (Orobanchaceae) genera are susceptible. Connectivity in both groups of heteroecious hosts has facilitated the spread of the pathogen into northwestern America (Brar *et al.*, 2015).

## 2. Dependence and effect of symbiosis

The magnitude of the cost or benefit of an interaction for the plant, including the extent to which the plant depends on the interaction to complete its life cycle, also determines which interaction motifs are likely to influence invasion. For example, the disruption of weak mutualisms may be overcome through reduced plant dependence, whereas strong mutualisms are more likely to lead to mutualism limitation or co-invasion as factors in invasion.

Does the strength of interaction between invasive host plant and their fungal associates consistently differ from the strength of native plant–fungal interactions? In the case of mutualisms, both enhanced and reduced mutualisms have been proposed. However, in their meta-analysis of arbuscular mycorrhizal plants, Bunn *et al.* (2015) found that alien hosts showed no difference in average growth response to mycorrhizas compared with native plants. The range of invasive plant responses observed was a subset of the range of native plant responses, suggesting that alien plants do not exploit arbuscular mycorrhiza in novel ways where they invade. Many successful invasive species benefit weakly from associations with arbuscular mycorrhizal fungi (Klironomos, 2003; Pringle *et al.*, 2009; Seifert *et al.*, 2009; Vogelsang & Bever, 2009) as do many successful natives (Janos, 1980).

Plant–pathogen interactions are based on a molecular dialogue shaped by co-evolutionary processes (Jones & Dangl, 2006), while novel associations lack this co-evolutionary history. For simple host–pathogen interactions, theoretical models predict that the negative effect of pathogens on host fitness evolves to an intermediate level optimizing pathogen fitness (Lenski & May, 1994; Cressler *et al.*, 2016). Novel associations between alien pathogens and native plants and vice versa may therefore have more variable effect sizes than co-evolved associations. In particular, toxin-based plant defences may have stronger effects on naïve novel pathogens, increasing disease resistance, while elicitor-receptor-based plant defences may fail to recognize novel pathogens, making plants more susceptible to disease (Verhoeven *et al.*, 2009). However, not all new host–pathogen encounters lead to severe disease. For example, Tobias *et al.* (2016) reported a full range of plant phenotypes, from full susceptibility to immunity, in terms of plant response to alien *Puccinia psidii* (myrtle rust) in >50 species in the Myrtaceae family in Australia. Introduced pathogens that cause

few or nonsevere symptoms are much less likely to be detected or reported than pathogens causing widespread mortality, thus distorting our perspective of the impact of introduced pathogens.

Taken as a whole, there is little evidence for consistent shifts in the average effect sizes of novel pathogen associations versus co-evolved associations, although a higher variance in effects of novel associations may be more likely to lead to host extinction than co-evolved associations. Expecting any consistent shift in effect size may be naïve in any case, given the diversity of plant–fungal associations within the broad category of mutualist or pathogen and the various factors influencing the evolution of virulence and resistance (Parker & Gilbert, 2004; Cressler *et al.*, 2016). Notwithstanding this, understanding the size of the effect on hosts is important in anticipating which interaction motifs are more or less likely within each interaction type (Table 4).

In considering the effect size of plant–fungal interactions and interaction motifs, it is important to consider environmental context. Invasive species often occur in disturbed and high-nutrient environments (MacDougall & Turkington, 2005) and all invasions occur in the context of global climate change. High-nutrient environments can reduce the relative benefits of mycorrhizal associations (Johnson, 1993, 2010) and hence potentially reduce the effect of mutualist limitation, or promote invasion by nonmycorrhizal and weakly mycorrhizal plants (reduced dependence) at the expense of strongly mycorrhizal established plants (Allen *et al.*, 2016; Marshall *et al.*, 2016). Disturbance may also favour the invasion of plants with lower mycorrhizal dependence as a result of reductions in arbuscular mycorrhizal abundance, with examples in alien and native agricultural weeds (Rinaudo *et al.*, 2010). By contrast, some forms of disturbance may increase the abundance or impact of pathogens. *Sphaeropsis sapinea*, for example, can shift from an endophytic lifestyle to having strong negative effects as a serious pathogen on pines under stress conditions, such as drought or hail damage (Wingfield *et al.*, 2001). Finally, moisture availability may influence plant–fungal invasion dynamics. Although plants typically show increased responsiveness/dependence on arbuscular mycorrhizal fungi in more arid environments, invaders can be less dependent on fungi for drought tolerance than natives (Endresz *et al.*, 2015).

## V. Spatial context of linked plant–fungal invasions

Invasion inherently involves dispersal, and many symbiotic fungi disperse independently of their host plant. Differences in the dispersal of plant and fungal symbionts may cause spatial patchiness in plant–fungal interactions, potentially driving different interaction motifs at the invasion front (Moeller *et al.*, 2015) or across geographical barriers. A lack of fungal symbionts at the forefront of invasions may limit plants strongly dependent on co-invasive mutualists (e.g. pines; Nuñez *et al.*, 2009), may favour the formation of novel associations with native fungi (Moeller *et al.*, 2015), or may promote the invasion of plants otherwise limited by natural enemies (Diez *et al.*, 2010).

Dispersal asymmetry is likely to be particularly important in plant–fungal co-invasions, depending on the dispersal dynamics of both plants and fungi. The wind-dispersed, small spores of many



fungi favour long-distance dispersal (Brown & Hovmøller, 2002; de Wit & Bouvier, 2006), and long-distance dispersal of fungi is common (Moyersoen *et al.*, 2003; Barberán *et al.*, 2015; Davison *et al.*, 2015; Urcelay *et al.*, 2017). Nonetheless, dispersal limitation can be important in many fungi, including ectomycorrhizal fungi (Peay *et al.*, 2012; Peay & Bruns, 2014), arbuscular mycorrhizal fungi (Spence *et al.*, 2011), and *Phytophthora* (Jules *et al.*, 2002).

Animal dispersal appears important in fungal co-invasions, including mammalian dispersal of mycorrhizal fungi (Nuñez *et al.*, 2013), and insect dispersal of alien pathogens forming novel associations with native plants (Wingfield *et al.*, 2010). In some cases, alien invasive animals form novel associations with either alien (co-xenic novel associations) or native fungi, greatly increasing fungal spread (Wingfield *et al.*, 2010; Wood *et al.*, 2015). Given the vast numbers of wind-dispersed spores that many fungi produce (Peay *et al.*, 2012), the importance of animal dispersal in multiple invasions seems curious. It is possible that animal-dispersed species may be more likely to encounter compatible hosts and/or spores of compatible mating types than species with potentially longer distance, but more diffuse dispersal by wind. Humans also clearly facilitate invasions by dispersing fungi to new regions and spreading fungi within regions after introductions (Dickie *et al.*, 2016). In many cases, human-mediated dispersal is unintentional, for example when live plants are moved with soil and associated biota (Jules *et al.*, 2002; Liebhold *et al.*, 2012), but fungi are also intentionally introduced and spread for biocontrol (Ellison *et al.*, 2008; Winston *et al.*, 2014) and to promote the growth of plants (Schwartz *et al.*, 2006; Vellinga *et al.*, 2009; Nuñez *et al.*, 2015).

At larger spatial scales, abiotic factors may also result in patchiness in plant–fungal interactions across the invasion. Where fungal distributions are more limited by environmental factors than their host, plant–fungal co-invasion may be limited to a subset of the total invaded range of the plant. In particular, when host-specific fungal pathogens have failed to establish over the entire range of an invasive host (Evans & Bruzese, 2003), this may be because a specific introduced pathogen strain is incompatible with the environment, although other factors such as host genetic structure may be important. Similarly, the co-xenic novel association of *Q. rubra* and *Phytophthora cinnamomi* in France is limited by winter temperatures, which restrict the range of the tropical-origin pathogen to a subset of the range of the plant host (Marçais *et al.*, 2004). Global change, particularly increased temperature and altered moisture regimes, may both facilitate fungal range expansion and increase plant stress (Anderson *et al.*, 2004; Woods *et al.*, 2005), potentially expanding plant–fungal interactions to a greater proportion of the plant's invaded range. While these dynamics have been documented in pathogens, we are unaware of any evidence of asymmetric climate limitation of co-invasive mutualistic fungi and their hosts.

## VI. Impacts of linked plant–fungal invasions on ecosystem processes

Some of the major ecosystem impacts of linked plant–fungal invasions are driven by changes in functional traits. Co-invasion of plants and fungi, in particular, can result in entirely new

ecosystem functions (Nuñez & Dickie, 2014). Ectomycorrhizal plant–fungal co-invasions into nonectomycorrhizal ecosystems, for example, may release nutrients from recalcitrant pools through fungal enzymatic pathways, resulting in a loss of soil carbon and at least short-term movement of nutrients from recalcitrant into available pools (Chapela *et al.*, 2001; Chen *et al.*, 2008; Dickie *et al.*, 2014). Similarly, novel associations of alien pathogens with native plants can have an immediate and powerful impact on biogeochemical cycling if they disproportionately impact hosts with unique biological pathways such as nitrogen (N) fixation (Ellison *et al.*, 2005; Ruess *et al.*, 2009). Pathogens can also cause long-term compositional change, through novel associations, spillover and spillback, with effects dependent both on the traits of the species that are lost and the traits of the species that replace them. Lovett *et al.* (2006), for example, observed that the long-term ecological consequences of *Neonectria* beech bark disease are likely to depend on whether beech, *Fagus grandifolia*, is replaced by *Acer*, with less recalcitrant litter than *Fagus*, or *Tsuga*, with more recalcitrant litter.

Other ecosystem-level impacts of linked plant–fungal invasions result from large changes in total plant biomass, which can be increased by mutualist fungi (Dickie *et al.*, 2011) or decreased by pathogens (Mitchell, 2003; Cobb & Rizzo, 2016; Preston *et al.*, 2016). In a broad sense, invasive mutualists may increase plant biomass and hence litter input, while pathogens may result in at least temporary pulses of increased litter and inputs of coarse wood (Cobb *et al.*, 2012). However, shifts in biomass and plant composition are probably the most critical drivers of change in ecosystem processes (Ehrenfeld, 2010; Cobb & Rizzo, 2016; Preston *et al.*, 2016). Perhaps the most obvious examples are the catastrophic losses of foundation species that succumb to alien pathogens (e.g. chestnut in North America), or the high-biomass invasion of some arbuscular mycorrhizal plants, facilitated by familiar associations with established, widespread fungi (Moora *et al.*, 2011; Spence *et al.*, 2011). Increased biomass as a consequence of invasion by mycorrhizal plants can result in increased carbon fixation and nutrient uptake and subsequent increased litter fall, increased water use and increased fuel load and fire risk (Gómez-Aparicio & Canham, 2008; Dickie *et al.*, 2011). Often the ecosystem trajectory is then modified to favour growth of ruderal (weedy) plants (Ehrenfeld, 2010; Simberloff *et al.*, 2013), including further invasion (Dickie *et al.*, 2014). Pathogen effects, which might be expected to reduce biomass, can be counterintuitive (Eviner & Likens, 2008) with the potential for pathogens to contribute to self-thinning or successional change from grasslands to woody vegetation (Van der Putten *et al.*, 1993), and hence increase rather than decrease ecosystem-level plant biomass. Because the ecosystem effects of linked plant–fungal invasions are often mediated by changes in soils, their legacies may persist even where invasive species are removed (Grman & Suding, 2010; Corbin & D'Antonio, 2012; Dickie *et al.*, 2014).

## VII. Management implications

Understanding plant–fungal interactions can improve all stages of management of linked plant–fungal invasions, ranging from risk

assessment to ecosystem restoration. Further investigation of linked plant–fungal invasions may improve management of new invasions, allow us to mitigate the impacts of invasive plants and fungi, and improve evaluation of both positive and negative effects of invasions (e.g. provision of ecosystem services; Dickie *et al.*, 2016).

At present, most plant risk assessment is based on the assumption that plant and fungal traits are static. Greater recognition is needed of the potential for plant traits to change following co-invasion or formation of novel associations with fungi, including increased or decreased invasiveness depending on mutualist or pathogen accumulation (Diez, 2005; Diez *et al.*, 2010; Dickie *et al.*, 2016). Some fungi are deliberately introduced for biological control or to promote plant growth. A better understanding of spillover and spillback processes, particularly in the context of changing environmental conditions, will help improve assessments of the potential beneficial and detrimental effects of these translocations (Schwartz *et al.*, 2006; Nuñez *et al.*, 2015; Blackburn & Ewen, 2016).

When managing established invasive plants, individuals are frequently removed without a clear strategy for restoration. Both invasive plants and their associated fungi modify environmental conditions, potentially resulting in post-removal re-invasion or invasion by other alien species as a result of legacies associated with plant–fungal interactions (Dickie *et al.*, 2014). Managing legacies of disrupted fungal communities as a result of linked plant–fungal invasions, whether through co-invasion (including spillover) or mutualism disruption, may be a key step in promoting successful restoration. Facilitation across multiple invasive plant species may also occur through shared mutualists (including co-xenic novel associations). Conversely, there may be cases where alien plants can facilitate restoration of native vegetation by hosting compatible

mutualistic fungi, although at least one test found no such effect (Dickie *et al.*, 2014). Understanding the dependence of fungi on plants (including alternate hosts) and their ability to persist in the absence of hosts may be key to developing strategies for managing fungal invasions (Goheen *et al.*, 2012; Dickie *et al.*, 2016).

## VIII. Conclusions

Linked plant–fungal invasions spanning the spectrum from mutualistic to pathogenic interactions share common fundamental motifs which warrant their consideration within a united ecological framework. Here, we have attempted to: (1) highlight the diversity, ecological importance and potential complexity of plant–fungal invasions; (2) categorize this diversity into broadly applicable, simplified motifs that apply to both mutualistic and pathogenic interactions; (3) apply these motifs to the invasion process and demonstrate the potential effect of these interactions on the outcomes of plant invasions; (4) consider the effects of symbiont specificity, dependence, effect size, and the abiotic environment on the type or strength of interactions; and (5) consider mechanisms by which linked plant–fungal invasions influence ecosystem-level impacts and management outcomes. Linked plant–fungal processes can be critical to determining the outcomes and impacts of both plant and fungal invasions, yet research in these areas remains limited (Dickie *et al.*, 2016; Preston *et al.*, 2016).

Our synthesis of the current knowledge of linked plant–fungal invasions reveals a number of key research questions, with regard to long-term dynamics, biogeographical comparisons, and ecosystem-level impacts (Table 5). Interaction motifs provide a starting point for integrating case studies to search for generalizations across

**Table 5** Key questions arising from a consideration of linked plant–fungal invasions

Biogeography	Do plant–fungal interaction motifs change following introduction to a new range, or do interactions largely mimic those found in the native range? How common are novel interactions compared with re-established interactions from the native range (co-introduction or familiar associations)? Is co-invasion more common in long-distance translocations (e.g. cross-hemisphere) than short-distance translocations (Bahram <i>et al.</i> , 2013)?
Long-term trajectories	How does the complexity of plant–fungal interactions change over time in an invasion? Are three- and higher node interactions more common with longer time following introduction? To what extent do changes in plant–fungal interactions, including evolutionary adaptation, explain long-term declines in plant invasions? Are boom-and-bust cycles of invasive plants related to the accumulation of fungal interactions? To what extent is interaction accumulation driven by co-invasion vs novel associations?
Ecosystem context and impacts	How strongly are plant–fungal interactions context-dependent on interactions with other biota, including competition (e.g. Waller <i>et al.</i> , 2016), animals driving fungal reproduction (e.g. Leuchtman, 2007) and dispersal (e.g. Nuñez <i>et al.</i> , 2013), or other biotic interactions? Do the impacts of a plant invasion change when the species identities or biogeographical origins of the fungal symbionts change (e.g. change in mycorrhizal partners)? How do the impacts of an invasion change over time, including through evolution of the invaded community (Lankau & Nodurt, 2013) or enemy accumulation (Flory & Clay, 2013; Stricker <i>et al.</i> , 2016)?
Management implications	How do linked plant–fungal invasions contribute to the development of legacy effects following invasive plant removal (Dickie <i>et al.</i> , 2014)? Can a better understanding of the biological interactions between plants and fungi be harnessed to improve management of either plant or fungal invasions (Dickie <i>et al.</i> , 2016)?
Extension to other systems	To what degree are the motifs and outcomes of linked plant–fungal invasions specific to fungi, and what are the key similarities with and differences from viruses (Faillace <i>et al.</i> , 2017), bacteria, protists, parasitic plants, and animal interactions during plant invasions?

invasions and to answer some of these questions. The motifs we discuss here conceptualize the complexity of interactions, provide concrete hypotheses to guide future work, and establish a framework for investigating the role of the environmental and biotic context in mediating plant–fungal interactions and their impact on invasion dynamics. Some of these motifs have already been widely studied (e.g. enemy release; Jeschke, 2014), while others are more hypothetical or constructed from only one or a few examples (e.g. symbiont displacement) and their real world applicability and generality remain to be shown.

Using interaction motifs as a guide, future research pursuing fundamental questions in linked plant–fungal invasions can bring fresh insight into invasion dynamics and reveal the role of previously overlooked fungal interactions in driving observed patterns in plant invasions. Studying linked plant–fungal invasions also provides a framework for further elucidating fungal invasion dynamics and evaluating their impacts in the context of community and ecosystem-level processes. The pervasive nature of plant–fungal interactions and the potential diversity and importance of these interactions in driving invasions highlights the need to explicitly consider these interactions in future work in invasion ecology.

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