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The Role of Pathogens in Plant Invasions

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Abstract

Plant–pathogen interactions occur throughout the process of plant invasion; pathogens can acutely influence plant survival and reproduction, while the large densities and spatial distributions of invasive plant species can influence pathogen communities. However, interactions between invasive plants and pathogens are often overlooked during the early stages of invasion. As with introductions of invasive plants, the introduction of agricultural crops to new areas can also generate novel host–pathogen interactions. The close monitoring of agricultural plants and resulting insights can inform hypotheses for invasive plants where research on pathogen interactions is lacking. This chapter reviews the known and hypothesized effects of pathogens on the invasion process and the effects of plant invasion on pathogens and infectious disease dynamics throughout the process of invasion. Initially, pathogens may inhibit the transport of potentially invasive plants. After arrival in a new range, pathogens can facilitate or inhibit establishment success of introduced plants depending on their relative impacts on the introduced plants and resident species. As invasive plants spread, they may encounter novel pathogens and alter the abundance and geographic range of pathogens. Pathogens can mediate interactions between invasive plants and resident species and may influence the long-term impacts of invasive plants on ecosystems. As invasive plants shift the composition of pathogen communities, resident species could be subject to higher disease risk. We highlight gaps in invasion biology research by providing examples from the agricultural literature and propose topics that have received little attention from either field.

11.1 Overview

Microbial communities of plants influence plant health and ecological interactions. The microbial communities of invasive non-native plants (invasive plants, hereafter) change as plants leave behind some microbes from their native ranges, including pathogens, and acquire new symbionts in their introduced ranges (Colautti

et al., 2004; Gilbert and Parker, 2006; Flory and Clay, 2013). It is well accepted that microbes associated with (or absent from) introduced plants, and soil microbial communities in particular, can influence initial plant establishment and subsequent impacts on resident species (van der Putten, 2010). For example, establishment of invasive pine species in Argentina was limited until mutualistic mycorrhizal fungi were introduced

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(Nuñez *et al.*, 2009), while the loss of soil pathogens may have promoted widespread and dense establishment of the black cherry tree (*Prunus serotina*) in Europe (Reinhart *et al.*, 2003) and spotted knapweed (*Centaurea maculosa*) in the USA (Callaway *et al.*, 2004). By contrast, garlic mustard (*Alliaria petiolata*) reduced native plant growth in US forests by suppressing microbial mutualists (Stinson *et al.*, 2006), which may have facilitated its own spread.

Although the ecological role of microbes in plant invasions is increasingly understood, microbial communities of invasive plants can change over time, altering the long-term dynamics and impacts of invaders (Lau and Suwa, 2016; Stricker *et al.*, 2016). Changes in microbial communities may be as straightforward as an invasive plant acquiring a pathogen from a resident species in its introduced range, or as complex as the evolution of microbes that are exposed to novel selection pressures during the introduction process (e.g. surviving transport and new environmental conditions, Fig. 11.1). Pathogens can be particularly influential microbes, affecting plant mortality, reproduction and competitive ability (Dobson and Crawley, 1994; Mordecai, 2011). Consequently, pathogens that infect crops have long received attention from researchers and practitioners. Like invasive plant species, agricultural plants are introduced to new geographical regions where new host–pathogen associations can arise and their interactions with pathogens can change over time. Therefore, case studies from agricultural plant pathology may provide important insights for understanding the relationships between invasive plants and their pathogens.

Using the stages of plant invasion as an organizational framework, we identify specific points where pathogens can exert influence (Fig. 11.1). First, pathogens may accompany and determine survival of hosts during transport to new geographic regions. During establishment and spread, introduced and native pathogens can alter plant survival and reproduction, as well as influence interactions with resident species. Invasive plants may facilitate the spread or emergence of plant pathogens as the plants reach uninvaded regions and interact with resident plant species. Pathogens can promote or attenuate the impact of invasive plant populations on resident species through altered

ecological interactions or shifts in ecosystem functions. Finally, pathogen effects on invasive and resident species can change over time due to pathogen accumulation and evolution.

In this chapter, we review key research advances in understanding how pathogens affect and are affected by invasive plants. We use the stages of invasion (i.e. transport, establishment, spread, ecological impacts) to consider invasive plant–pathogen interactions and how they change over time (Fig. 11.1), highlight key examples from the invasive species and agricultural plant pathogen literature, and outline future research needs. The relationships between invasive plants and pathogens are relevant to multiple significant areas of invasion biology research that also consider plant–herbivore interactions (e.g. the Enemy Release Hypothesis, the Biotic Resistance Hypothesis and biological control, Gilbert and Parker, 2006). We cover such topics briefly and point readers to corresponding chapters in this book for more in-depth analyses. Given the burgeoning volume of global travel and commerce that provides continuous opportunities for transport of potential invaders into almost all habitats, elucidating how pathogens can modify interactions between invasive and resident species is more pressing than ever.

11.2 Transport

11.2.1 The role of pathogens in non-native plant transport

The deliberate or inadvertent transport of non-native plants to new ranges can include the movement of seeds, plant parts, juveniles and adult plants across geographic boundaries (Lehan *et al.*, 2013; Chapman *et al.*, 2017). Pathogens may affect the transport of non-native plants directly by affecting plant survival (Ragaert *et al.*, 2007; Kumar and Kalita, 2017), or indirectly, by facilitating the targeting of individual plants for quarantine or removal by human agents (Colautti *et al.*, 2004; Hulme *et al.*, 2008). Invasive plants are most frequently transported for ornamental trade (Lehan *et al.*, 2013), and often in the form of live plants (Chapman *et al.*, 2017). Invaders

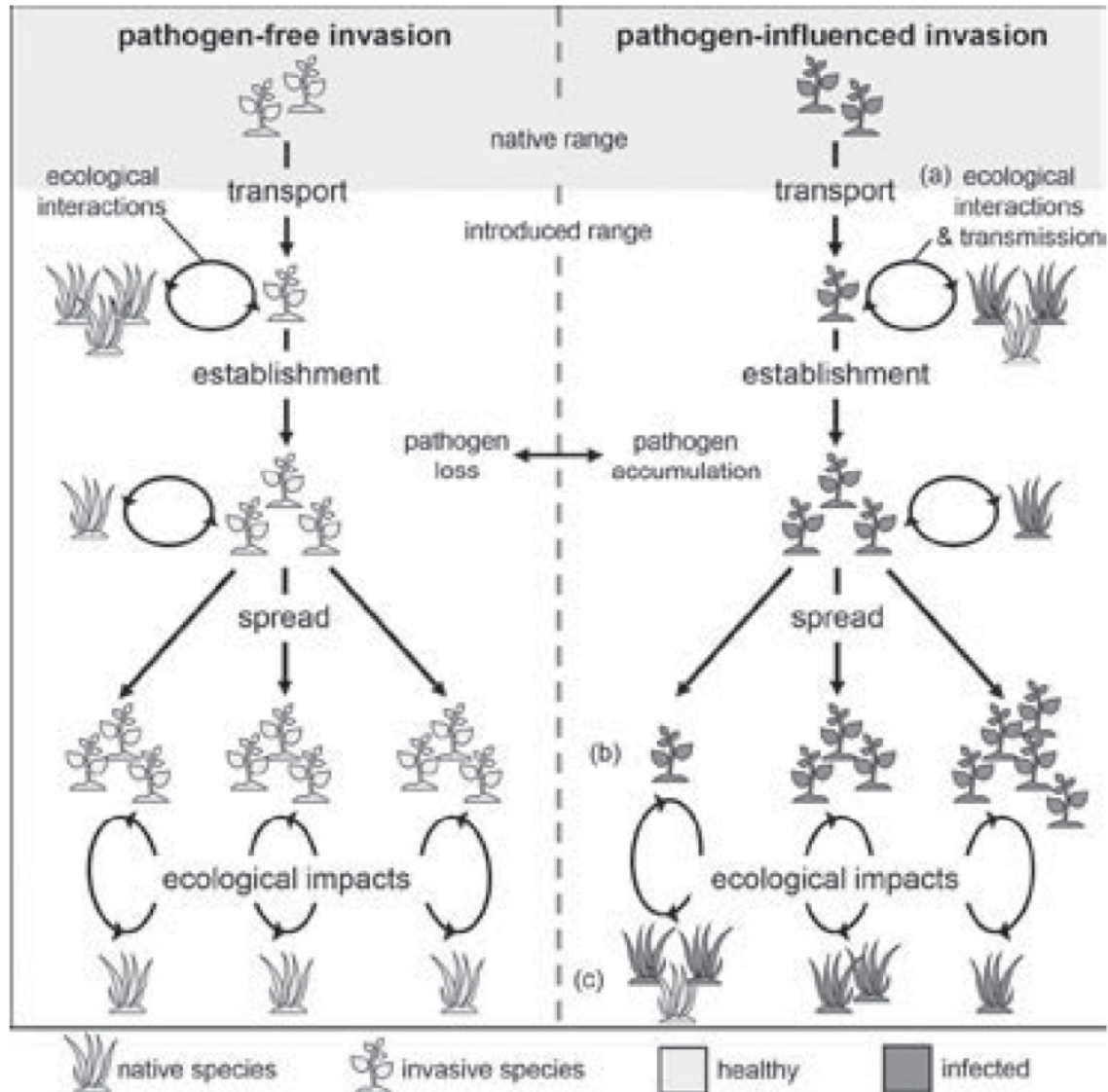


Fig. 11.1. Potential impacts of pathogens on the plant invasion process. Plants may complete the invasion process in the absence of pathogens (left panel), in the presence of pathogens (right panel), or by moving between these two states (pathogen loss and accumulation). Evidence from agricultural crops suggests that pathogens may affect survival of introduced plant populations throughout the invasion process. Examples from both invasive species and crops demonstrate pathogen loss following transport and pathogen accumulation following establishment (centre double-headed arrow). Curved arrows represent ecological interactions with resident plants, including competition and, when pathogens are present, transmission (a). Pathogens can be co-introduced with invasive species or transmitted from resident species. Pathogens may alter the size of established invasive plant populations through direct or indirect processes, including competition with native species (b). Studies on invasive plants have shown that pathogens can mediate competition with resident species through changes in invasive population size or disease transmission (c). Pathogen communities and infection prevalence may shift with the invasion process and exposure to new environments and hosts.

tend to be transported as seeds when movement is unintentional, contaminating soil or agricultural seeds (Lehan *et al.*, 2013). Pathogen infection of seeds and live plants

during storage and transportation contributes to crop losses (Ragaert *et al.*, 2007; Kumar and Kalita, 2017) and may alter the survival of invasive plants during transport.

11.2.2 Transport of Plant Pathogens

The simultaneous or sequential introduction of two non-native species (i.e. a plant and a pathogen) is known as ‘co-introduction’, and ‘co-invasion’ if they both become invasive (Dickie *et al.*, 2017). Multiple methods exist to ensure introduced plants are disease-free, such as inspection, quarantine and sanitation of imported plants (Colautti *et al.*, 2004; Hulme *et al.*, 2008). Pathogens that cause obvious symptoms, kill plants or are detected with screening methods are more likely to be destroyed than those that go unnoticed by remaining dormant or causing symptoms later in the plant’s life cycle (Liebhold *et al.*, 2012). In addition, plants transported during a specific life stage (e.g. seeds, juveniles) will lack pathogens that specialize on other life stages (Barrett and Heil, 2012). It is through these filters that co-introduction of certain classes of pathogens that have coevolved with invasive plants may be prevented (Keane and Crawley, 2002; Colautti *et al.*, 2004).

While screening methods can limit the transport of pathogens, there are numerous examples of pathogens being introduced despite prevention efforts. Some of the most devastating pathogens of crops and native species were transported on seeds, logs and live plants (Elmer, 2001; Brasier, 2008; Liebhold *et al.*, 2012). The origins and timing of introduction, however, are unclear for the majority of invasive plant pathogens (Desprez-Loustau *et al.*, 2007), making post hoc identification of co-introduction cases difficult. Nevertheless, some recently introduced invasive plant populations are infected with pathogens (Mitchell *et al.*, 2010; Stricker *et al.*, 2016), suggesting co-introduction or rapid acquisition, and there are numerous examples of co-introduced animals and parasites (Lymbery *et al.*, 2014).

Recurring transport or movement of individuals (i.e. propagule pressure) can help plants, and their microbes, overcome barriers to introduction (Lockwood *et al.*, 2005). For example, it is hypothesized that repeated importations of Japanese chestnut trees to North America resulted in the ultimate introduction of the chestnut blight fungus (*Cryphonectria parasitica*, Dutech *et al.*, 2012). Sudden oak death (*Phytophthora ramorum*), another virulent tree pathogen, was

likely introduced to North America and Europe through repeated importations of nursery stock (Grünwald *et al.*, 2012).

11.3 Establishment: Survival and Reproduction

Following transport, introduced plants must survive and reproduce to become established (Blackburn *et al.*, 2011). Barriers such as small initial population size, limited resource availability, unfavourable climate, absence of a key mutualist and high herbivory can constrain plant establishment (Levine *et al.*, 2004; Lockwood *et al.*, 2005; Bradley *et al.*, 2010). It is hypothesized that introduced or resident pathogens can reduce survival and reproduction of introduced plants as well (i.e. biotic resistance, Elton, 1958), but evidence for such inhibitory interactions is limited (Levine *et al.*, 2004; Strauss *et al.*, 2012). For co-introduced pathogens to become established, they must be able to overcome multiple ecological and evolutionary barriers (Desprez-Loustau *et al.*, 2007). While the ecological impacts of invasive plants often occur well after the plant has established, the co-introduction of pathogens creates the opportunity for more immediate impacts on resident species, impacts that can spread spatially well beyond the geographic range of the introduced host (e.g. chestnut blight spread rapidly through essentially the entire range of the American chestnut, past the sites of introduction of the likely initial host, introduced Asian chestnuts, Dutech *et al.*, 2012).

11.3.1 The role of pathogens in non-native plant establishment

Co-introduced pathogens or those rapidly acquired from resident plants could prevent an introduced plant from becoming established (Elton, 1958), but these processes are rarely documented in ecological studies due to small population sizes and limited impacts of introduced plants during the establishment phase, which can keep these systems ‘below the radar’ of applied ecologists (Strauss *et al.*, 2012). Similar outcomes can occur, however, during monoculture production of non-native agricultural or

forest crop plants, and novel disease pressures can hamper production (i.e. prevent ‘invasion’). For example, the fungus *Dothistroma pini* spread through young plantations of the non-native pine *Pinus radiata* in Eastern and Central Africa between 1940 and 1965, damaging foliage, slowing tree growth and forcing foresters to substitute *P. radiata* for other species (Gibson, 1972). *D. pini* may have been introduced to the region through long-distance natural dispersal or air traffic (Gibson, 1972).

Resident pathogens can indirectly aid introduced plants by infecting resident species and reducing competition. The Enemy Release Hypothesis (Chapter 10, this volume) posits that the absence of pathogens and other types of enemies in the introduced range leads to greater performance or competitive ability of non-native species relative to the native range (Elton, 1958; Gillett, 1962; Keane and Crawley, 2002; Colautti *et al.*, 2004). Indeed, plants in introduced ranges tend to have fewer recorded pathogens than those in the native ranges (Mitchell and Power, 2003; Blumenthal *et al.*, 2009) and invasive plants can suffer less pathogen-induced damage and mortality than do resident species in the introduced range (Hawkes, 2007; Han *et al.*, 2008; Chun *et al.*, 2010; but see Blaney and Kotanen, 2001; Parker and Gilbert, 2007). In addition, crops tend to experience a ‘honeymoon’ period of limited pathogen pressure when initially planted in a new region (Bebber *et al.*, 2014a). However, few studies have connected lower pathogen pressure on invasive plants in their introduced range to higher population growth rates (Dunn *et al.*, 2012) or ultimate abundance or spatial extent of the invasion.

The nature and magnitude of disease impacts on introduced plant establishment are mediated by many factors, including pathogen specificity and phylogenetic relatedness of the introduced plant to resident species (Parker and Gilbert, 2004). Plant pathogen host ranges can vary widely, from a single plant species, such as the rust fungus *Puccinia chondrillina* used as a biocontrol for skeleton weed (*Chondrilla juncea* L.) in Australia (Cullen *et al.*, 1973), to rich arrays of phylogenetically distinct host species, such as the globally-distributed oomycete *Phytophthora cinnamomi*, which is native to Southeast Asia and can infect nearly 5000 plant species (Hardham and Blackman, 2018).

Host range specificity depends on both coevolution between pathogen infection strategies and plant defences, and environmental conditions (Barrett and Heil, 2012). Introduced plants that fall within the host ranges of resident generalist pathogens or are closely related to hosts of more specific pathogens are more likely to experience disease during and after establishment (Parker *et al.*, 2015; Crous, 2017).

The invasion process is likely to influence the magnitude of disease impacts through changes in disease resistance in the introduced plant population. The genetic bottleneck often associated with non-native plant transport may lead to low genetic diversity in secondary metabolites or disease resistance genes of introduced plant species (Dlugosch and Parker, 2008), promoting eventual disease spread. In contrast, infection-induced mortality during transport or establishment may select for disease resistance (Blaney and Kotanen, 2001; Gos *et al.*, 2012). Multiple introductions can reintroduce genetic variation into the introduced plant population (Gladieux *et al.*, 2011), but each introduction may also bring novel pathogens and novel genotypes of established pathogens from the native range (Dutech *et al.*, 2012; Grünwald *et al.*, 2012).

11.3.2 Establishment of co-introduced plant pathogens

Because host population sizes can affect the ability of specialist pathogens to establish (Anderson and May, 1979), co-introduced pathogens may be limited by the initially small population size of their introduced plant host. However, pathogens may overcome this barrier through multiple mechanisms. Pathogens with broad host ranges can infect resident species while their introduced plant host is establishing and increasing in abundance (Strauss *et al.*, 2012), potentially with devastating effects. For example, the bacterium *Xylella fastidiosa* was introduced to southern Italy on ornamental plants from Central America and caused rapid mortality of historically important and quite old olive trees (Marcelletti and Scortichini, 2016). In addition, pathogens may remain dormant while the introduced plant species is establishing, only

to emerge later in favourable conditions. For example, *P. ramorum* produces resting spores that can survive adverse environmental conditions (Tooley *et al.*, 2008).

Pathogens with specific requirements, such as insect vectors or narrow environmental tolerance, may face barriers to establishment. Viruses of crops have a more limited global distribution than their fungal counterparts, likely due to their dependence on insect vectors that are less widely distributed (Bebber *et al.*, 2014a). Environmental conditions may also differ greatly between the native and introduced ranges and could impact pathogen establishment. Honeysuckle leaf blight (*Insolibasidium deformans*) requires specific temperature and humidity conditions to infect its host, which may contribute to determining its geographic distribution and the timing of infection on invasive Amur honeysuckle (*Lonicera maackii*, Boyce *et al.*, 2014).

11.4 Spatial Spread: Dispersal and Repeated Establishment

The spread of invasive plants within an introduced range involves dispersal and repeated establishment events. Dispersal can occur through natural or human-assisted movement of seeds, plant parts and individuals (Reichard and White, 2001; Padayachee *et al.*, 2017), and establishment across space depends on complex interactions among plant traits, propagule pressure, landscape structure and environmental factors such as temperature and precipitation (Catford *et al.*, 2009). Because dispersal and repeated establishment are similar to transport and initial establishment, respectively, many of the plant–pathogen interactions that occur during those phases are relevant to spatial spread. However, pathogen impacts on short-distance dispersal can uniquely affect spatial spread.

11.4.1 The role of pathogens in invasive plant spread

Pathogens can influence the dispersal of invasive plants in ways similar to how they affect initial plant transport to the introduced range.

For example, intentional movement of seeds or plants by humans is likely to select for visibly healthy individuals (Reichard and White, 2001). Movement within the introduced range differs from initial transport because it can involve more localized dispersal mechanisms, including animals, wind, water and machinery (Horvitz *et al.*, 2017). The infection status or defensive compounds of plants may affect animal foraging behaviour and resulting seed dispersal (Cazetta *et al.*, 2008). Pathogens also can affect plant size, seed size and seed production rates (Dobson and Crawley, 1994), which influence natural and unintentional dispersal (Thomson *et al.*, 2011; Tamme *et al.*, 2014).

Just as pathogens can induce mortality and reduce fecundity during initial plant establishment in a new range, pathogens also can inhibit establishment in new areas within the introduced range. Simple models of invasion suggest that in a homogeneous landscape, the wave of advance moves with a velocity proportional to \sqrt{rD} , where r is intrinsic growth rate, and D gauges the rate of diffusive dispersal (Andow *et al.*, 1990). A pathogen that reduces r is expected to reduce the rate at which an invasive plant moves through the landscape. This same qualitative expectation also holds in more complex models of invasion (Neubert and Parker, 2004). Moreover, environmental conditions mediate plant–pathogen interactions, such that the barrier to establishment caused by disease is likely to vary over space and time. For example, environmental variation drove differences in pathogen resistance between two ecotypes of native Australian flax (*Linum marginale*), leading to spatial differences in disease prevalence and host–pathogen coevolution (Laine *et al.*, 2014).

11.4.2 Pathogen community changes with spatial spread

As invasive plants spread, they may acquire new pathogens and maintain others through simultaneous or independent dispersal. The effectiveness of independent pathogen dispersal can vary by mechanism. For example, aphids, an important vector of plant viruses, can disperse up to hundreds of metres per day through wind-assisted movement, but frequently crawl

among leaves on a single plant (Irwin *et al.*, 2007). Wind-dispersed fungal pathogens, however, may have even higher spread rates than those that depend on insects, as is the case for some invasive pathogens of US forests (Evans and Finkral, 2010). Plants may also lose some of their pathogens through the process of spatial spread (Chalkowski *et al.*, 2018), acquiring new pathogen communities as they encounter different species due to greater geographic range, habitat diversity and residence time (Clay, 1995; Mitchell *et al.*, 2010). Crop pathogens tend to accumulate as the intensity of cultivation increases (Bebber *et al.*, 2014b), while continuing to be limited by phylogenetic relatedness to resident species (Crous, 2017).

11.5 Ecological Impacts

Invasive plants can have significant impacts on resident communities and ecosystems. One of the most well-supported impacts of invasive plants is reduced diversity in the resident plant community (Vilà *et al.*, 2011; Pyšek *et al.*, 2012), which frequently arises through competition (Levine *et al.*, 2003). Pathogens can alleviate or enhance the negative effects of plant resource competition (Mordecai, 2011; Flory and Clay, 2013), which has been explored across a range of systems (Bradley *et al.*, 2008; Bagchi *et al.*, 2014; Spear and Mordecai, 2018). Invasive plants can also impact other aspects of the ecosystem, such as associated animal communities (Bateman and Ostoja, 2012), nutrient cycling (Allison and Vitousek, 2004) and fire regimes (Flory *et al.*, 2015), but the role of pathogens in mediating such impacts on communities and ecosystems has rarely been studied.

11.5.1 Pathogen-mediated plant competition

As invasive plants establish, resident plant communities can experience competition for shared resources (Brown *et al.*, 2002), allelopathy (Callaway and Ridenour, 2004) and damage from shared enemies (Dangremond *et al.*, 2010), ultimately leading to shifts in plant community diversity and structure. Pathogens can influence

the ecological impact of invasive plants by altering the competitive abilities and niche overlap of native and invasive species (Mordecai, 2011). Theoretically, pathogens can push the outcome of competition between native and invasive plants in three directions: coexistence, competitive exclusion of the invasive species and competitive exclusion of the native species (Louda *et al.*, 1990; Mordecai, 2011; Flory and Clay, 2013).

Because the competitive exclusion of one species by another is a long-term process, a common approach to understanding the possible dynamics is to parameterize mathematical models with experimentally-derived values (Eppinga *et al.*, 2006; Borer *et al.*, 2007; Fabiszewski *et al.*, 2010; Mordecai, 2013). Such models have provided insights into pathogen-mediated competition. For example, the invasive marram grass (*Ammophila arenaria*) suffers from negative plant–soil feedbacks in its native and introduced ranges (Beckstead and Parker, 2003). Model predictions suggest that generalist pathogens that accumulate in *A. arenaria* soil can promote the exclusion of native species if native species incur more infection-induced fitness costs than *A. arenaria* (Eppinga *et al.*, 2006). In addition, invasive cheatgrass (*Bromus tectorum*) promotes infection of native squirreltail grass (*Elymus elymoides*) seeds (Beckstead *et al.*, 2010). However, modelling suggests that the pathogen does not promote competitive exclusion of the native squirreltail grass, partly due to its higher resistance to infection than the invasive species (Mordecai, 2013).

Short-term experiments often motivate the use of models to predict the outcome of pathogen-mediated competition (Malmstrom *et al.*, 2005; Beckstead *et al.*, 2010). Experiments with garlic mustard (*A. petiolata*, Cipollini and Enright, 2009) and stiltgrass (*Microstegium vimineum*, Stricker *et al.*, 2016) each suggest that foliar fungal pathogens could favour recovery of native species, while experiments with reed grass (White *et al.*, 2018) and Siam weed (*Chromolaena odorata*, Mangla and Callaway, 2008) suggest that soil pathogens contribute to the competitive exclusion of native species. Using data from such experiments to parameterize mathematical models can aid predictions about how pathogen impacts on native and invasive species can alter the outcome of competition, and how

these outcomes may be modified by evolution, environmental conditions and other ecological interactions.

In addition to naturally occurring pathogens, intentionally introduced pathogens can modify interactions between native and invasive plants. Biological control (biocontrol) programmes introduce enemies that are specific to invasive plants and reduce their competitive effects on native species (Chapter 20, this volume). Fungal pathogen biocontrol agents can be highly effective, establishing quickly across large geographic areas and greatly reducing invasive plant abundance (Burdon *et al.*, 1981; Trujillo, 1985). Their efficacy can be sensitive to environmental conditions, such as precipitation (Cullen *et al.*, 1973) and the presence of competing plant species (Abu-Dieyeh, 2007; Meiri *et al.*, 2010). Successes and failures of biocontrol can signal potentially important factors to consider when evaluating the outcomes of natural pathogen accumulation.

11.5.2 Plant–pathogen interactions and broader effects

While it is clear that invasive plants can influence resident species through disease transmission, they may also indirectly promote disease through habitat modification (Chalkowski *et al.*, 2018). For example, dense plant invasions can change temperature, humidity and solar radiation, creating conditions favourable for fungal growth and sporulation (Burdon and Chilvers, 1982; Young *et al.*, 2012). High plant density can also reduce dispersal distances required for pathogens to infect new plants (Clay, 2008) and invasive plants can release chemicals into the soil that promote disease prevalence (Mangla and Callaway, 2008).

High invasive plant abundance also can affect other trophic levels and ecosystem functioning. Invasive plants can alter animal communities, trophic interactions, primary productivity, nutrient cycling and disturbance regimes (Levine *et al.*, 2003; Vilà *et al.*, 2011; Guiden and Orrock, 2017). Pathogen impacts on invasive plant fitness can mediate such effects. For example, reduced plant cover due to disease can affect soil formation and water regulation

(Cheatham *et al.*, 2009). Disease-induced mortality of trees can increase the intensity of forest fires (Forrestel *et al.*, 2015) and alter nutrient cycling through food webs (Smock and MacGregor, 1988). Invasive species (Batten *et al.*, 2006) and pathogens (Essarioui *et al.*, 2019) can both affect the composition of soil microbial communities, but their combined effects are unclear.

11.6 Long-term Dynamics

The impacts of pathogen accumulation on invaded plant communities are likely to occur over long time periods because it can take years or decades for invasive plants to reach influential densities and experience epidemics (Enright and Cipollini, 2007; Stricker *et al.*, 2016). It is common for the enemy communities of invasive plants, consisting of herbivores and pathogens, to increase in diversity and damage over time (Table 11.1, Hawkes, 2007; Schultheis *et al.*, 2015). In many cases, the ideal long-term outcome (from a management perspective) of pathogen accumulation on an invasive plant species would be decline of the invasive species and recovery of the native species. However, there are both ecological and evolutionary causes for lags in pathogen effects on invaders and their interactions with native species (D'Antonio and Flory, 2017).

11.6.1 Long-term ecological dynamics of invasive plants and their pathogens

The accumulation of host-specific pathogens on an invasive species could lead to its decline and the recovery of native species (Flory and Clay, 2013). While there are few recorded examples of natural pathogen-driven population crashes of invasive plants (Simberloff and Gibbons, 2004), similar dynamics have occurred in agricultural systems, where crop failures can be driven by epidemics (Desprez-Loustau *et al.*, 2007).

Legacy effects, including alterations to the soil microbial community or chemical composition, may prevent native species recovery following pathogen-induced invasive plant decline (Corbin and D'Antonio, 2012; D'Antonio and Flory, 2017). Indeed, changes in soil microbial

Table 11.1. Examples of natural pathogen accumulation (i.e. not as the result of the intentional introduction of agents for biocontrol) and impacts in invaded systems.

Invasive plant species	Pathogen species	Pathogen in native range?	Accumulation time	Disease impacts on invader	Disease impacts on community	References
<i>Ailanthus altissima</i> (tree-of-heaven)	<i>Verticillium albo-atrum</i> and <i>Verticillium nonalfalfae</i>	No (Asia)	~200 years	85% mortality	Negligible	Harris et al., 2013; Maschek and Halmischlager, 2018
<i>Alliaria petiolata</i> (garlic mustard)	<i>Erysiphe cruciferarum</i> (powdery mildew)	Yes (Europe)	~140 years	50% reduction in seed production	Eliminates the competitive impacts (reduced seed production) of garlic mustard on a native species	Enright and Cipollini, 2007; Cipollini and Enright, 2009
<i>Ammophila arenaria</i> (marram grass)	Soil fungi (e.g. <i>Fusarium</i> spp., <i>Alternaria</i> spp.)	Yes (Europe)	Unknown	16% reduction in germination, 13% reduction in seedling survival, and 81% reduction in biomass	Competitive exclusion of native possible if it is more sensitive to soil pathogens than <i>A. arenaria</i>	Van der Putten et al., 1993, an Van der Putten and Peters, 1997; Beckstead and Parker, 2003; Eppinga et al., 2006
<i>Avena fatua</i> , <i>Bromus hordeaceus</i> , and other annual grasses	Barley and cereal yellow dwarf viruses	Yes (Europe)	Unknown, but viruses are thought to have been established prior to plant introduction	89% reduction in biomass, 88% reduction in seed production	Disease can allow invasion by competitively inferior invasive species	Malmstrom et al., 2005, Malmstrom et al., 2007; Borer et al., 2007
<i>Bromus tectorum</i> (cheatgrass)	<i>Pyrenophora semeniperda</i> (black fingers of death)	Yes (Europe)	May have been simultaneously introduced	Can kill more than 80% of dormant seeds	Promotes coexistence between invasive and native grass	Beckstead et al., 2010; Stewart et al., 2009; Boose et al., 2011; Mordecai, 2013
<i>Cirsium arvense</i> (Canada thistle)	<i>Puccinia punctiformis</i> (rust fungus)	Yes (SE Europe, N Africa)	May have been simultaneously introduced	30–100% reduction in density	Unknown	Berner et al., 2013, 2015

Continued

Table 11.1. Continued

Invasive plant species	Pathogen species	Pathogen in native range?	Accumulation time	Disease impacts on invader	Disease impacts on community	References
<i>Lonicera maackii</i> (Amur honeysuckle)	<i>Insolibasidium deformans</i> (honeysuckle leaf blight)	No (W Asia)	Unknown	Stem dieback	Unknown	Riffle and Peterson, 1986; Boyce <i>et al.</i> , 2014; Farr and Rossman, 2015
<i>Microstegium vimineum</i> (stiltgrass)	<i>Bipolaris</i> spp. (foliar fungi)	Some species (S/E/SE Asia)	0–100 years	40–81% reduction in seed production	Increased native biomass through decreased invader biomass	Flory <i>et al.</i> , 2011; Stricker <i>et al.</i> , 2016
<i>Pueraria montana</i> var. <i>lobata</i> (kudzu)	<i>Phakospora pachyrhizi</i> (soybean rust)	Yes (E/SE Asia and Pacific)	~100 years	Negligible	Kudzu serves as an overwintering host for soybean rust, which kills soybeans	Harmon <i>et al.</i> , 2005; Fabiszewski <i>et al.</i> , 2010
<i>Rhododendron ponticum</i> (common rhododendron)	<i>Phytophthora ramorum</i> (sudden oak death)	Yes (Europe)	~240 years	Can be asymptomatic or cause foliar necrosis	Rhododendron acts as a reservoir host for the pathogen, which increases mortality of beech and other native woody species	Denman <i>et al.</i> , 2005, 2009; Purse <i>et al.</i> , 2013

communities and chemistry induced by invasive plants can negatively impact native plant performance (Callaway and Ridenour, 2004; Stinson *et al.*, 2006; Mangla and Callaway, 2008). In addition, invasive plant performance can be lower when grown in soil collected from conspecifics in the introduced range compared to sterilized soil or conspecifics in the native range, providing evidence for soil pathogen accumulation (Beckstead and Parker, 2003; Nijjer *et al.*, 2007; Diez *et al.*, 2010; McGinn *et al.*, 2018).

If pathogens suppress populations of invasive plants, extinction debt can still prevent the recovery of native species (Tilman *et al.*, 1994). A native plant population may be reduced to the point that its trajectory leads to extinction and it is unable to recover after the invasive plant no longer exerts strong competitive effects (Gilbert and Levine, 2013). However, native species richness tends to stay the same or increase following invasive plant removal (Andreu and Vilà, 2011; Abella, 2014), suggesting that extinction debt may be the exception rather than the rule.

11.6.2 Long-term evolutionary dynamics of introduced plants and their pathogens

While invasive plants and agricultural crops are ecologically similar in their initial release and accumulation of pathogens, invasive plants differ from most crops because they are free to evolve in response to accumulating pathogens. Indeed, invasive animals have evolved resistance to parasitoid and pathogen biological controls (Dwyer *et al.*, 1990; Tomasetto *et al.*, 2017). In addition, invaders may evolve tolerance to disease, as was demonstrated for European clover species introduced to California (Gilbert and Parker, 2010), and serve as a reservoirs for transmission to other plant species. In agricultural settings, wild plants can serve as pathogen reservoirs for crops (Wisler and Norris, 2005), including maintaining genetic variation in pathogen populations through diversifying selection (Meaden and Koskella, 2017). Coevolutionary dynamics between invasive plants and accumulating

pathogens may result in more long-term stability in the interaction than typically observed in the boom-and-bust cycles of disease in agricultural systems (McDonald and Linde, 2002; but see Simberloff and Gibbons, 2004), but this issue requires more systematic theoretical and empirical study. Evolutionary shifts in host range due to selection on host susceptibility, tolerance and pathogen traits is likely to lead to unpredictability in the ultimate abundance and geographical ranges of introduced species in their novel ranges.

11.7 Conclusions

The impacts of plant invasions and how they change over time can be mediated by their pathogen communities, which are themselves dynamic due to exposure to new environments, host species and microbial communities. While our understanding of invasive plant–pathogen interactions is driven by studies conducted after the invasive plant has established, insights from agricultural and natural systems suggest that biotic resistance to establishment, initial pathogen accumulation and long-term plant–pathogen coevolution can have important consequences for plant populations. Studies that evaluate the relative importance of pathogens (or absence of pathogens) and other factors on the process and impacts of invasion are needed to improve context and generality for the processes reviewed in this chapter. For example, experimental invasions combined with different types of ‘enemy removal’ treatments could allow for comparisons of the relative effects of soil-borne pathogens, foliar pathogens, insects and larger herbivores on the impacts of invasive plants (Borer *et al.*, 2015). In addition, studies on interactions between pathogens and other factors, such as herbivores (Swope and Parker, 2010) and resource availability (Heckman *et al.*, 2016), as well as anthropogenic drivers such as land use change, are needed to generate more realistic predictions about the long-term dynamics of invasive species.

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