

PLANT–MICROBE–INSECT INTERACTIONS

Plant pathogens structure arthropod communities across multiple spatial and temporal scales

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Summary

1. Plant pathogens and herbivores frequently co-occur on the same host plants. Despite this, little is known about the impact of their interactions on the structure of plant-based ecological communities.
2. Here, we synthesize evidence that indicates that plant pathogens may profoundly impact arthropod performance, preference, population dynamics and community structure across multiple spatial and temporal scales.
3. Intriguingly, the effects of plant–pathogen–herbivore interactions frequently cascade up and down multiple trophic levels and explain variation in the arthropod community at spatial scales ranging from patterns within single host plants to entire landscapes.
4. This review indicates that knowledge on pathogen–herbivore interactions may be crucial for understanding the dynamics of terrestrial communities.

Key-words: indirect defence, indirect interactions, multitrophic levels, plant-fungus-insect, plant–microbe–insect, trait–mediated interactions, tripartite interactions

Introduction

Plants in natural populations and agricultural fields are often attacked by a diverse community, including both herbivores and pathogens (Fig. 1; Strong, Lawton & Southwood 1984; Agrios 2005). These attacks are known to elicit major phenotypic changes in plants (Kessler & Baldwin 2002; Robert-Seilaniantz, Grant & Jones 2011). Hence, one would expect direct and indirect interactions to occur among herbivores, among pathogens and also between herbivores and pathogens (Fig. 2). However, while the role of plant-mediated pathogen–pathogen interactions in structuring pathogen communities has been a cornerstone in plant pathology for at least half a decade (Yarwood 1959; Kuć 1982), and plant-mediated herbivore–herbivore interactions are – after a heated debate (Hairton, Smith & Slobodkin 1960; Murdoch 1966) – recognized as a major structuring force in herbivore communities (Denno, McClure & Ott 1995; Kaplan & Denno 2007), the interactions between pathogens and herbivores have received relatively little attention. Such neglect of the role of plant-mediated pathogen–herbivore interactions may be due to two historic reasons. First, the

individual development of the disciplines of phytopathology and entomology has, despite several attempts of bridging both fields (e.g. Barbosa 1991; Stout, Thaler & Thomma 2006; Pieterse & Dicke 2007), so far resulted in relatively limited cross-disciplinary experimentation, mostly addressing phytohormonal signalling (Stout, Thaler & Thomma 2006; Pieterse & Dicke 2007; Schenk *et al.* 2008) up to the present day. To take an egg from our own basket, the first author wrote an entire PhD thesis on insect communities on the pedunculate oak (*Quercus robur*) before turning his attention to an abundant plant pathogen (the powdery mildew *Erysiphe alphitoides*) that frequently covers >20% of oak leaves in late autumn (Tack 2010; Tack, Gripenberg & Roslin 2012a). Indeed, we would not be surprised if many more entomologists ignore, or protect their experimental plants from, infection by plant pathogens, whereas many phytopathologists ignore, or protect their plants from, attack by herbivores. Secondly, one of the classic tenets of competition theory states that competition is strongest among closely related species (Darwin 1859; Gause 1934). While the latter view has received only weak support in a recent quantitative review on plant-feeding insect communities (Kaplan & Denno 2007), it may well have discouraged attempts to investigate cross-kingdom interactions. In this perspective, we explore

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Fig. 1. Plants are often simultaneously attacked by pathogens and herbivores. The photograph shows a black mustard leaf (*Brassica nigra*) with damage by a bacterial pathogen and feeding damage by cabbage white caterpillars (*Pieris brassicae*). Photograph courtesy Hans Smid, www.bugsinthepicture.com.

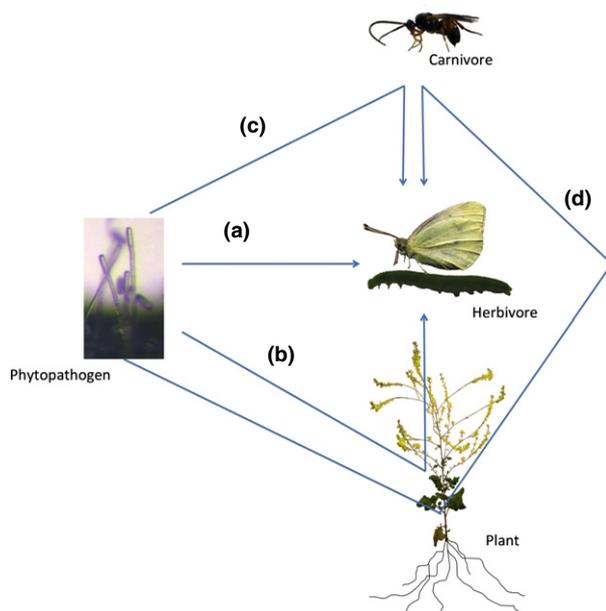


Fig. 2. The hypothetical impacts of a pathogen on the performance of herbivorous insects. The pathogen can (a) directly affect the performance of the herbivore, (b) affect the herbivore indirectly through the shared host plant, (c) affect the behaviour of the natural enemy and thereby indirectly affect the herbivore or (d) affect the herbivore through a plant-mediated response that in turn affects the natural enemies.

the current literature to exemplify how pathogens may impact herbivore communities across multiple spatial and temporal scales. We hope that such a synthesis will stimulate a diversity of future work on plant–pathogen–insect interactions.

The impact of pathogens on herbivore performance

An accumulating body of literature illustrates that pathogen infection of a plant can have a positive (Kennedy 1951; Vega *et al.* 1995; Siemens & Mitchell-Olds 1996; Friedli & Bacher 2001; Cardoza *et al.* 2003a; Mondy & Corio-Costet 2004; Cardoza & Tumlinson 2006), a negative (McIntyre, Dodds & Hare 1981; Karban, Adamchak & Schnathorst 1987; Hatcher *et al.* 1994a; Lappalainen, Helander & Palokangas 1995; Tinney *et al.* 1998; Stout *et al.* 1999; Kruess 2002; Rostás & Hilker 2002) or no effect on herbivore performance (Apriyanto & Potter 1990; Ajlan & Potter 1991; Stout *et al.* 1999). Strikingly, the impact of pathogens ranges from the immediate cessation of aphid reproduction on virus-infected *Zinnia* plants (Lowe & Strong 1963) to leafhoppers that can only survive on virus-infected aster plants (Maramorosch 1958). Such interactions between pathogens and herbivores may be direct (e.g. by the consumption of spores, mycelium or toxic fungal compounds), mediated by the host plant or mediated by natural enemies (Fig. 2). Here, we first explore these different ways in which pathogens may affect herbivore performance.

Direct interactions between plant pathogens and herbivores may be negative (McNee *et al.* 2003) or positive (Mondy & Corio-Costet 2004) for herbivore performance. For example, herbivorous larvae of the moth *Lobesia botrana* feeding on an artificial diet containing the phytopathogenic fungus *Botrytis cinerea* exhibited a higher survival, faster development and increased fecundity (Mondy & Corio-Costet 2004), thereby explaining the attraction of larvae to infected grapes (Mondy *et al.* 1998b). Indeed, several insect species prefer to, or have specialized in, feeding on fungal tissues (Yarwood 1943; Powell 1971; English-Loeb *et al.* 1999), suggesting that fungal tissue may be nutritious for insects. Unfortunately, the majority of papers do not conclusively demonstrate the role of direct interactions as such interactions can easily be confounded with plant-mediated effects (see below). For example, both direct feeding on rust and rust-mediated changes in plant quality may cause the lower fecundity (c. 55% less eggs laid) of the leaf beetle *Gastrophysa viridula* when feeding on rust-infected leaves from *Rumex crispus* and *Rumex obtusifolius* (Hatcher *et al.* 1994a).

Plant-mediated interactions between the pathogen and herbivore may take place when the pathogens and herbivores do not overlap spatially or temporally (Karbon & Baldwin 1997; Kessler & Baldwin 2002; Pieterse & Dicke 2007). As outlined by Rostás, Simon and Hilker (2003), such plant-mediated interactions can take place locally (between different parts within the same leaf) or more spatially separated (between leaves on the same plant). At the local scale, many studies do not allow disentangling direct and plant-mediated interactions, as herbivores were (potentially) feeding on “pathogen” tissue (see also Rostás,

Simon & Hilker 2003). As a solution, several studies have infected only part of the leaf, allowing the insect to feed on the uninfected part of the same leaf (Apriyanto & Potter 1990; Stout *et al.* 1999; Simon & Hilker 2003). Other studies have used plant pathogens and insects that feed on different plant tissues within the same leaf, thereby preventing any direct interactions (Johnson *et al.* 2003; Tack, Gripenberg & Roslin 2012a). For example, aphids (*Eucera-phus betulae*) feeding on the phloem of fungus-infected silver birch leaves were heavier, larger and displayed enhanced embryo development (Johnson *et al.* 2003). Likewise, the leaf miner *Tischeria ekebladella*, whose larvae live and feed in the mesophyll of oak leaves, showed an increased growth rate when feeding on oak leaves infected by oak powdery mildew (an ectoparasitic pathogen that only penetrates the epidermal cells; Tack, Gripenberg & Roslin 2012a).

Crucially, several studies have shown that the systemic effect of pathogen infection extends beyond the infected leaf (Siemens & Mitchell-Olds 1996; Cardoza *et al.* 2003a; Simon & Hilker 2003; Stout, Thaler & Thomma 2006; Röder, Rahier & Naisbit 2007; but see Apriyanto & Potter 1990). For instance, McIntyre, Dodds & Hare (1981) were the first to demonstrate that pathogen-induced systemic acquired resistance (by tobacco mosaic virus, TMV) could affect herbivore (*Myzus persicae*) performance. Likewise, TMV-infected plants may reduce the larval growth of the tobacco hornworm (*Manduca sexta*) (Hare 1983; Ajlan & Potter 1992). Nonetheless, the impact of pathogens on herbivores may also be positive. For example, the size of the leaf mine of the diamondback moth *Plutella xylostella* was higher on cotyledons inoculated or systemically induced by the fungal pathogen *Leptosphaeria maculans* (causal agent of blackleg disease; Siemens & Mitchell-Olds 1996). Taken together, plant-mediated interactions between plant pathogens and herbivores appear to play a largely overlooked – but quantitatively important – role by increasing or decreasing the performance of herbivores within plants.

While plant-mediated interactions have received increasing attention, several studies suggest that pathogens may also modify the interaction between the herbivore and its carnivorous natural enemies (Biere *et al.* 2002; Cardoza, Teal & Tumlinson 2003b; Rostás & Hilker 2003; Tack, Gripenberg & Roslin 2012a; Ponzio *et al.* this issue). For example, fungal infection may change the volatile composition of host plants (Schütz *et al.* 1999; Cardoza, Alborn & Tumlinson 2002; Cardoza & Tumlinson 2006; Rostás *et al.* 2006; Dötterl *et al.* 2009; Shapiro *et al.* 2012), which may in turn have a direct impact on the attraction of parasitoids (Turlings & Wäckers 2003). Indeed, Cardoza, Teal & Tumlinson (2003b) showed that the larval parasitoid *Cotesia marginiventris* landed more frequently on peanut plants that were damaged by the noctuid beet armyworm as well as infected by the white mould fungus *Sclerotium rolfsii* than on plants that were damaged by beet armyworm but not infected by the fungus. This behaviour seems adaptive, as the moths of the beet armyworm laid

more eggs on infected peanut plants. In another example, Biere *et al.* (2002) and Biere & Honders (2006) demonstrated that the fungal pathogen *Microbotryum violaceum* dramatically reduced the enemy-free space of the specialist seed predator *Hadena bicruris*, possibly explaining the reduced rate of oviposition on diseased plants. Overall, these studies suggest that parasitism rate is likely to vary between infected and noninfected host plants. Another study shows that the infection of the host plant may modify the immune defence of the herbivore against its parasites. For example, mustard leaf beetles (*Phaedon cochleariae*) feeding on *Alternaria brassicae*-infected Chinese cabbage leaves suffered increased larval mortality by a generalist entomopathogen (from 54% on control leaves to 100% on infected leaves; Rostás & Hilker 2003).

We note that several alternative mechanisms for altered parasitism rates in the presence of plant pathogens are worth exploration. For example, as plant pathogens frequently affect the developmental rate of larvae (Hatcher *et al.* 1994a; Laine 2004; Tack, Gripenberg & Roslin 2012a), pathogen infection of a plant may also cause a mismatch (or match) between herbivore and parasitoid/parasite phenology. Moreover, parasitoids may be attracted or deterred by the detection of visual, olfactory or textural stimuli from the pathogen (Ajayi & Dewar 1983; Honda, Ishiwatari & Matsumoto 1988).

The impact of plant pathogens on herbivore preference

Herbivores can show many types of behavioural responses, with either no effect (Moran 1998), attraction to (Barbe 1964; Lewis 1979; Mondy *et al.* 1998a,b; Friedli & Bacher 2001; Shapiro *et al.* 2012), or avoidance of (Krause & Raffa 1992; Hatcher *et al.* 1994a; Moran & Schultz 1998; Tinney *et al.* 1998; Kluth, Kruess & Tscharncke 2001; Rostás & Hilker 2002) pathogen infection when feeding or ovipositing. Consequently, pathogens may affect the distribution of herbivores and feeding damage among plants.

The distribution of eggs of herbivores across the landscape has a pronounced impact on the spatial distribution of individual herbivore species. This distribution, in turn, can be affected by pathogen infection status of the host plant. In a pioneering paper, Honda, Ishiwatari & Matsumoto (1988) showed that moths were attracted to an agar-cultured fungal-baited oviposition substrate in a laboratory cage experiment, thereby demonstrating the direct effect of fungal volatiles on insect movement. Interestingly, many studies have shown either an increase (Mondy *et al.* 1998a; Friedli & Bacher 2001) or decrease (Hatcher *et al.* 1994a; Moran & Schultz 1998; Kluth, Kruess & Tscharncke 2001; Rostás & Hilker 2002; Simon & Hilker 2005; Tack, Gripenberg & Roslin 2012a) in oviposition rates on infected leaves or plants.

Herbivores are well known to show selectivity with respect to the plants and plant parts they are feeding on (Schoonhoven, van Loon & Dicke 2005). A variety of

behavioural responses that mediate such food selection have been described. For example, the leaf beetle *Cassida rubiginosa* preferred feeding on healthy over *Phoma destructiva*-infected *Cirsium arvense* thistle plants (Kruess 2002). A further example shows that larvae may also move in relation to pathogen infections. Here, an olfactometer experiment demonstrated that larvae of the moth *Lobesia botrana* are attracted to the volatiles emitted by fungal-infected fruits of the grapevine *Vitis vinifera*, which partly explains the higher density of larvae on fungal-infected grapes (Mondy *et al.* 1998b).

In many insects, resource quality may determine group cohesion and spatial distribution of larvae. Laine (2004) demonstrated that larval groups of the Glanville fritillary butterfly *Melitaea cinxia* split up more frequently into smaller groups when feeding on a powdery mildew-infected host plant (*Plantago lanceolata*). As overwintering survival depends on group size, this may then have an impact on overwintering survival of the butterfly population (Laine 2004). In another study, Hatcher *et al.* (1994a) demonstrated that the beetle *G. viridula* showed more spatial aggregation (percentage larvae in close proximity) when feeding on healthy leaves as compared to rust-infected leaves.

To conclude, these results demonstrate that pathogens may not only affect the performance of herbivores (as identified in the previous section), but pathogen infection may also modify the attraction (or deterrence) of infected plants to insect herbivores and herbivore spatial aggregation. As a consequence, pathogen infection may modify the spatial distribution of herbivores in the landscape.

The impact of plant pathogens on herbivore population dynamics

Given the changes in herbivore performance and preference imposed by pathogen infection, we may expect the latter to affect herbivore population dynamics. Indeed, several studies show that the herbivore reproductive rate can increase (Johnson *et al.* 2003), decrease (Karban, Adamchak & Schnathorst 1987; Apriyanto & Potter 1990) or be unaffected (Ajlan & Potter 1991) on pathogen-infected plants. For example, the aphid *E. betulae* had a higher population growth rate on pathogen-infected branches of the silver birch, possibly because of the higher concentration of free amino acids (Johnson *et al.* 2003). In contrast, spider-mite populations grew slower on healthy than fungal-wilt-infected cotton seedlings (Karban, Adamchak & Schnathorst 1987). The impact of the pathogen on herbivore population dynamics may also vary within the infected plant, as shown by the mite *Tetranychus urticae* on tobacco plants infected by tobacco necrosis virus: while the population dynamics were not affected by systemic induction, the total number of mite offspring was reduced by more than 35% on the leaf part that received the inoculation (Apriyanto & Potter 1990).

Although the studies mentioned above only cover a single or few generations, they demonstrate the important point that pathogen infection can change the population growth rate of herbivore populations. Other studies demonstrate how pathogen infection can affect the initial population growth after colonization and the carrying capacity of the plant (Kennedy 1951; Prüter & Zebitz 1991). As an example of the former, Kennedy (1951) demonstrated that populations of the black bean aphid *A. fabae* grew faster, the generation time was shorter and emigration began sooner on mosaic virus-infected sugar beets. As an example of changed equilibrium densities, Prüter & Zebitz (1991) showed that the equilibrium density of aphids (*Aphis fabae*), as based on the balance between reproduction, mortality and emigration, was reduced on rust-infected faba beans. Similarly, population density of the pea aphid *Acyrtosiphon pisum* was higher on healthy plants of several forage legumes (white clover, red clover and alfalfa) as compared to the same plant species infected with the root pathogen *Fusarium* (Leath & Byers 1977). In another 30-day free choice trial of the pea aphid, the population size was largest on healthy as compared to single or dually infected arrowleaf clover plants (*P. erythrosetica* and bean yellow mosaic virus; Ellsbury, Pratt & Knight 1985). This pattern was explained by both enhanced inter-plant aphid movement from infected to healthy plants and reduced reproductive rate on diseased plants. In summary, these studies demonstrate that the impact of pathogen infection on both the preference and performance of the herbivore may strongly affect the population dynamics of the herbivore.

The spatial scale of plant–insect–pathogen interactions

Pathogen infection exhibits spatial variation and usually differs between different parts of a single leaf, among leaves within individual plants, among plants and among plant populations (Burdon 1987). Because herbivores are well known to discriminate between their resource for feeding and oviposition at each of these spatial scales (Schoonhoven, van Loon & Dicke 2005), pathogens may then either directly or indirectly affect herbivore abundance and distribution across multiple spatial scales. Direct mechanisms may include tactile or visual perception of the pathogen, whereas indirect mechanism may involve pathogen-induced changes in the plant or natural enemies.

The herbivore may prefer or avoid feeding on the pathogen-infected tissue at the scale of a single leaf. For example, Barbe (1964) and Lewis (1979) observed that earwigs (*Dermaptera* sp.) and grasshoppers (*Melanoplus differentialis*) strongly preferred feeding on leaf parts with rust pustules and consequently consume very little leaf tissue. Indeed, given the fine scale of selective grazing, such interactions have been described as facultative mycophagy (Hatcher 1995). In contrast, the thistle tortoise beetle *Carduus thoermeri* and the true weevil *Trichosirocalus*

horridus strongly selected noninfected leaf parts of rust-infected thistle leaves to feed on (Kok, Abad & Baudoin 1996), and the leaf beetle *P. versicolora* consumed less leaf area from infected leaf halves as compared to uninfected halves of the same leaves in choice assays (Simon & Hilker 2005).

Several herbivore species discriminate between pathogen-infected and noninfected leaves, thereby modifying the abundance of species within single plant individuals (Zebitz *et al.* 1990; Hatcher *et al.* 1994a; Tinney *et al.* 1998; Simon & Hilker 2005; Röder, Rahier & Naisbit 2007; Tack, Gripenberg & Roslin 2012a). For example, the willow leaf beetle avoided ovipositing on rust-infected willow leaves (Simon & Hilker 2005). Other studies have focused on the distribution of the eggs within the whole plant. While the beetle *G. viridula* laid a similar number of eggs on rust-infected and healthy *R. crispus* plants, the distribution over the different leaf age classes differed strikingly, where a greater proportion was laid on the older, infected leaves, than on the equivalent aged leaves on the healthy plants (Hatcher *et al.* 1994a). In a comparable study, the aphid *A. fabae* shifted its distribution towards the older, rust-infected leaves on faba bean (Zebitz *et al.* 1990). A study by Johnson *et al.* (2003) gives additional insight in the movement process by showing that higher abundances of aphids (*E. betulae*) on rust-infected leaves of silver birch (*Betula pendula*) are due to lower emigration rates from rust-infected leaves, whereas colonization appears random with respect to rust infection.

Pathogen infection may also alter herbivore attraction at the scale of entire host plants, with either higher (Macias & Mink 1969; Apriyanto & Potter 1990) or lower (Macias & Mink 1969; Prüter & Zebitz 1991; Krause & Raffa 1992; Hatcher *et al.* 1994a; Kruess 2002; Simon & Hilker 2005; Röder, Rahier & Naisbit 2007; Zargaran, Erbilgin & Ghosta 2012; Ponzio *et al.* this issue) herbivore abundance on infected plants. For example, Simon & Hilker (2005) demonstrated that willow leaf beetles not only oviposited fewer eggs on rust-infected leaves, but herbivore preference also resulted in fewer eggs on infected willow saplings as compared to healthy saplings. In another example, both larvae and adults of the leaf beetles *O. elongata* and *O. cacaliae* emigrated more rapidly from rust-infected plants (*Adenostyles alliariae*) than from healthy plants (Röder, Rahier & Naisbit 2007). In contrast, striped cucumber beetles moved more frequently to virus-infected cucumber plants (Apriyanto & Potter 1990). At a larger spatial scale, performance, feeding and oviposition decisions may result in different densities of herbivores between pathogen-infected and healthy plant populations. However, no data are yet available at this spatial scale.

The temporal dimension of tripartite interactions

Several studies show how the interaction between a pathogen and herbivore depends on the time-scale of the

interaction. For example, it is well known that systemic acquired resistance induced by pathogens needs time to develop and may recede after a certain time period (e.g. McIntyre, Dodds & Hare 1981). Hence, the temporal match between herbivore and pathogen in the experimental setting may be crucial for the outcome of the interaction. As the exact temporal induction pattern is often unknown, and differs among pathogens, several researchers have replicated their studies over time (McIntyre, Dodds & Hare 1981; Peacock *et al.* 2003; Simon & Hilker 2005; Cardoza & Tumlinson 2006) or followed the interaction for a longer-time period (Kennedy 1951; Zebitz 1990). For example, the relative growth rate of the black bean aphid (*A. fabae*) was higher on rust-infected leaves as compared to healthy leaves, showing a distinct peak on infected leaves (and not on healthy leaves) at 19 days post-inoculation when secondary rust pustules erupted through the leaf epidermis (Zebitz 1990). Another temporal pattern is shown by the leaf willow beetle *P. versicolora*, which consumed similar amounts of leaf tissue on healthy and uninfected halves of rust-infected leaves 8–12 days after infection, but feeding decreased significantly on the uninfected leaf half after 16 days (Simon & Hilker 2005). At a much larger time-scale, Krause & Raffa (1992) used a feeding assay to demonstrate that larch sawfly larvae (*Pristiphora erichsonii*) quickly abandoned seedlings of the European larch *Larix decidua* that had been defoliated by the larch needle cast fungus in the previous year. Likewise, Lappalainen, Helander & Palokangas (1995) showed that the pupal weight of the autumnal moth *Epirrita autumnata* was reduced on spring foliage of the mountain birch *Betula pubescens* subsp. *tortuosa* when it was infected by the rust *Melampsorium betulinum* in the previous year. Overall, these studies demonstrate that pathogen infection may affect herbivores at multiple time-scales, ranging from several hours after inoculation to multiple years.

Species identity matters

The attack by a single member of the community results in major species-specific transcriptomic and physiological changes in a plant (Kessler & Baldwin 2002; Dicke 2009), resulting in changes in leaf quality and secondary chemistry. As different herbivore species are well known to respond differently to plant characteristics (Schoonhoven, van Loon & Dicke 2005; Ali & Agrawal 2012), we may expect them to respond differently to changes induced in the host plant (Poelman *et al.* 2010). Indeed, the literature reveals a striking variation in pathogen–herbivore interactions, with many study systems showing a positive (e.g. Carruthers, Bergstrom & Haynes 1986; Friedli & Bacher 2001) or negative (e.g. Karban, Adamchak & Schnathorst 1987) impact of the pathogen on the herbivore. Importantly, when different herbivores (within the same study system) respond differently to the presence of a plant pathogen, pathogens have the potential to play a key role in structuring the insect community. Likewise, the identity of

the pathogen and plant species may also play a crucial role in the impact of pathogens on insect community structure. Important insight is then given by the few studies that have used multiple herbivore, pathogen or plant species to disentangle the role of species identity of each kingdom in affecting the interaction outcome.

Several studies have shown that a single pathogen may differentially affect herbivore species (Pesel & Poehling 1988; Kok, Abad & Baudoin 1996; Röder, Rahier & Naisbit 2007; Mouttet *et al.* 2011; Tack, Gripenberg & Roslin 2012a). For example, a leaf miner and free feeder on the pedunculate oak responded differently to the presence of the very same plant pathogen: where the free feeder suffered decreased growth rate and pupal mass in the presence of oak powdery mildew *Erysiphe alphitoides*, mid-instar leaf miner larvae increased their growth rate (Tack, Gripenberg & Roslin 2012a). Likewise, females of the leaf beetle *O. cacaliae* favoured larviposition on healthy leaves, whereas the congeneric species *O. elongata* showed no significant preference (Röder, Rahier & Naisbit 2007). Mouttet *et al.* (2011) found a similar pattern, where aphid (*Rhodobium porosum*) population growth decreased on *Botrytis cinerea*-infected rose plants (*Rosa hybrida*), whereas thrips population growth was not significantly affected. Similarly, while female weevils (*Trichosirocalus horridus*) preferred to lay eggs on rust-infected leaves, the thistle tortoise beetle *Cassida rubiginosa* did not discriminate between healthy and rust-infected leaves during oviposition (Kok, Abad & Baudoin 1996). In a final example, the cereal aphid *Metopolophium dirhodum* produced fewer offspring on winter wheat (*Triticum aestivum*) infected by powdery mildew (*Erysiphe graminis*), whereas another cereal aphid (*Sitobion avenae*) showed the opposite response (Pesel & Poehling 1988). Such differences among species in response to the same pathogen can then be expected to frequently change the composition of the insect community in the presence of a plant pathogen: if one herbivore thrives and another not, this should affect their relative abundances.

A single insect species may also respond differently to a variety of pathogen species. This should hardly be surprising, given the differences in pathogen growth and pathogen chemistry (Agrios 2005) and changes among pathogens in the induction profile of even the same plant species (Nimchuk *et al.* 2003). Indeed, several studies have shown that pathogen species identity can have a large impact on the interaction with the herbivore (Macias & Mink 1969; Ellsbury, Pratt & Knight 1985; Honda, Ishiwatari & Matsumoto 1988; Stout *et al.* 1999). For example, *Helicoverpa zea* caterpillars strongly reduced their relative growth rate when feeding on *Pseudomonas syringae*-infected as compared to healthy tomato plants, whereas infection by *Phytophthora infestans* did not affect the performance of this herbivore (Stout *et al.* 1999). Likewise, the peach aphid *Myzus persicae* preferred feeding on sugar beet leaves infected with beet yellows virus (BYV) and beet western yellows virus (BWYV), but preferred symptomless leaves

over leaves infected by curly top virus (CTV; Macias & Mink 1969). In another striking example, larvae of the cinnabar moth *Tyria jacobaeae* feeding on common groundsel did not differentiate between healthy leaves and leaves infected with *Puccinia lagenophorae*. However, larvae consumed more than four times as much leaf tissue from healthy leaves as compared to leaves infected by *Coleosporium tussilaginis* (Tinney *et al.* 1998).

Interestingly, the developmental stage of the pathogen may also affect the response of the insects, thereby adding further spatial and temporal complexity. For example, the stem-boring weevil *Apion onopordi* laid more than twice as many eggs on systemic shoots of rust-infected thistle plants (*Cirsium arvense*) with the younger rust stage (bearing the pycnia) as compared to shoots from uninfected plants, but the pattern reversed when the rust developed further and produced asexual urediniospores (Friedli & Bacher 2001).

As even related plant species differ in their response to the same pathogens and herbivores (Kessler & Baldwin 2002), the interaction between herbivores and pathogens may be affected by the plant species (Hatcher *et al.* 1994a; Tinney *et al.* 1998). For example, infection of the common groundsel *S. vulgaris* with the rust pathogen *C. tussilaginis* did not affect the performance and feeding rate of cinnabar moth larvae, whereas infection of another plant species (*Tussilago farfara*) strongly reduced food intake and final larval weight and slowed down larval development (Tinney *et al.* 1998). Finally, Hatcher *et al.* (1994a) demonstrated that rust infection of *Rumex crispus* did not change the number of eggs laid by the beetle *Gastrophysa viridula*, whereas the number of eggs was reduced when leaves of the congeneric *R. obtusifolius* were infected with rust (*Uromyces rumicis*).

In summary, the sparse evidence to date strongly suggests that herbivores react differently to the same pathogen, the same herbivore reacts in different ways to different pathogens, and the interaction between the pathogen and herbivore strongly depends on the plant species on which the interaction takes place. Such species-specific responses are then likely to result in altered relative abundances of herbivores between healthy and pathogen-infected plants or plant tissue.

Pathogen–plant–insect interactions within a community context

In this section, we explore how the species-specific impact of pathogens on herbivore performance, preference and population dynamics may shape – by at least two mechanisms – the structure of the entire herbivore food web, ranging from phytophagous arthropods, slugs and vertebrates to higher trophic levels like parasitoids and predators. Moreover, we show that the pathogens may have a strong impact on the spatial dynamics of this multitrophic plant-based food web. Finally, we argue that – at least in some cases – we need to take into account the diverse

plant-based community surrounding our focal three-way interaction.

At least two nonmutually exclusive hypotheses may explain the impact of pathogens on the herbivore community. First, as outlined in the previous section, species-specific responses of herbivores to the presence of pathogens are likely to result in differentiation in herbivore community structure between infected and healthy plants and plant tissue in the field. Secondly, herbivores early in the season may be attracted, unaffected or deterred by plant pathogens, with potentially cascading effects on the herbivore community in the remainder of the season. For example, if pathogens would mediate variation in early-season herbivore colonization (or absence of colonization due to deterrence), then this may predictably and strongly modify the structure of the subsequent insect community (Van Zandt & Agrawal 2004; Poelman *et al.* 2008, 2010). Indeed, when a single competitive species is deterred by a plant pathogen, this may increase the abundance and diversity of other herbivore species. In contrast, when a keystone herbivore (e.g. a galler or leaf folder; Crawford, Crutsinger & Sanders 2007; Wang, Marquis & Baer 2012) is deterred by the presence of a plant pathogen, we may expect a decrease in the diversity of the herbivore community. Given the natural phenology of pathogens and insects in the field, we may also expect that only certain species, or certain generations in multivoltine insects, will be affected by the plant pathogen.

Several observational studies offer support for the contention that pathogens have a pronounced impact on community structure in the field (Kluth, Kruess & Tschardt 2001; van Nouhuys & Laine 2008; Tack, Gripenberg & Roslin 2012a). For example, the structure of insect communities differed between healthy and rust-infected (*Puccinia punctiformis*) creeping thistles (*Cirsium arvense*; Kluth, Kruess & Tschardt 2001). While the abundance of aphids and several beetle species increased on rust-infected plants, a comparable number of species preferred uninfected plants. Likewise, two independent studies reported that the community structure of a large number of endophagous insects was differentially affected by the intensity of infection of oaks with powdery mildew (Tack, Gripenberg & Roslin 2012a; Zargaran, Erbilgin & Ghosta 2012).

Pathogens also – directly or indirectly – affect the composition of the broader (nonarthropod) herbivore community. For example, rust-infected plants have been reported to either attract (Ramsell & Paul 1990; De Nooij, Biere & Linders 1992) or deter (De Nooij, Biere & Linders 1992) feeding by slugs. Moreover, pathogen infection can lead to changes in the performance of even large mammals. For instance, infection of rye (*Secale cereale*) by the rust pathogen *Puccinia recondita* increased the concentration of nitrate, thereby making the plant poisonous for cattle (Piening 1972). Likewise, infection of the same and related plant species by *Claviceps* species has resulted in more than a hundred epidemics of human ergotism between the 6th and 18th century, which may have had a strong effect on

fertility trends in the UK and other European countries in the 17th and 18th centuries (Bennett & Klich 2003 and references therein). Moreover, the pathogen still forms a risk for domestic animals like cattle, sheep, pigs and chickens.

While most studies have sampled only herbivores, pathogens may also affect higher trophic levels (Kluth, Kruess & Tschardt 2001; van Nouhuys & Laine 2008; Tack, Gripenberg & Roslin 2012a). For example, pathogens may affect parasitoid abundance and herbivore parasitism rates (Ponzio *et al.* 2013). As an example of changes in parasitoid abundance, the presence of the leaf miner *T. ekebladella* on oak leaves infected by powdery mildew decreased the abundance of parasitoids emerging from these leaves in the following year (Tack, Gripenberg & Roslin 2012a). Moreover, pathogen infection can change the performance and population dynamics of the parasitoids: individuals of the braconid parasitoid *C. melitaearum* weighed less when the host (*M. cinxia*) was fed with mildew-infected leaves than when it was fed healthy leaves (van Nouhuys & Laine 2008). Moreover, the sex ratio of parasitoid offspring emerging from host larvae that were fed with infected leaves was biased towards females. Given that pathogens may thus affect both herbivore community structure and herbivore–parasitoid interactions, we may then expect that a single phytopathogen may ultimately modify the entire plant–pathogen–insect food web. While we know of no example involving a phytopathogen, such a mechanism is illustrated by a study on endophyte infection of the grass *Lolium multiflorum* (Omacini *et al.* 2001). Here, the endophyte changed the relative abundance of two aphid species, the rate of parasitism by secondary parasitoids and – most fascinatingly – the structural characteristics of the food web. That pathogens may modify herbivore–natural enemy food webs is further suggested by a study on the insect community on creeping thistles. While the predator/prey ratio was more than 50% higher on uninfected as compared to systemically rust-infected creeping thistles, coleopteran and heteropteran predators were more abundant on infected plants. This pattern suggests a pathogen-mediated change in predator community structure (Kluth, Kruess & Tschardt 2001).

While rarely studied, pathogens may affect the colonization-extinction dynamics of the herbivores across several spatial scales. For example, given the widely different response of herbivores to the presence of powdery mildew on oak, and the decreased colonization of trees by the leaf miner *T. ekebladella* on trees with heavy powdery mildew infection, it seems likely that the pathogen modifies the spatial dynamics of the herbivore community (Tack, Gripenberg & Roslin 2012a). Another study shows how the spatial dynamics of a multitrophic interaction can change across the landscape: while populations of the Glanville fritillary butterfly went extinct more frequently in mildew-infected plant patches (Laine 2004), pathogen infection increased the colonization success of its parasitoid *C. melitaearum* (van Nouhuys & Laine 2008).

Finally, we need to realize that plants are frequently attacked by multiple pathogens, and plants are members of diverse plant communities. As many plants are attacked by multiple pathogens, the plant landscape may become even more heterogeneous for the herbivore, where plants may have different diseases or multiple infections. Importantly, as herbivores are likely to respond idiosyncratically to each plant disease (and likely to multiple infections), we may expect additional spatial complexity that can structure the herbivore community. Likewise, the structure of the plant community may affect pathogen–plant–insect interactions. For example, as many insect species feed on multiple host species, pathogen infection may not only change the distribution of eggs among individuals of the same plant species, but also the egg distribution among individuals of different plant species present within the same community. For example, Hatcher & Ayres (1997) showed that the leaf beetle *G. viridula* preferred feeding on *R. obtusifolius* as compared to *R. crispus*, but the infection of the former host plant species nullified this preference. Interestingly, this also suggests that in some cases there may be a cost to pathogen resistance, as the absence of pathogen infection will increase the intensity of insect herbivory. However, as pathogens can also positively affect herbivore performance and abundance, we may expect that in such scenarios, an increased resistance to pathogens will simultaneously decrease herbivory, thereby increasing the selection intensity for pathogen resistance. Finally, plant diseases may frequently affect plant density and the composition of the plant community (Burdon 1987), which is well known to affect herbivore communities, thereby creating another mechanism by which pathogens may affect the herbivore community.

Overall, we find scant but convincing evidence that pathogen infection may affect the structure and spatial dynamics of multitrophic plant-based food webs, including several types of herbivores (arthropods, slugs and vertebrates) and natural enemies like parasitoids and predators. Moreover, the realization that plants are attacked by multiple pathogens, and plant species grow in complex plant communities, may add additional insight in the role of pathogens in structuring herbivore communities.

Future directions

Our synthesis of the literature illustrates that pathogen–plant–insect interactions are common, diverse and important. Indeed, it appears that the impact of pathogens on herbivores can be as strong, or even stronger than, interactions among herbivores themselves (Karban, Adamchak & Schnathorst 1987; Stout *et al.* 1999; Kaplan & Denno 2007; Mouttet *et al.* 2011; Tack, Gripenberg & Roslin 2012a; but see Ajlan & Potter 1992). Given the diversity of both pathogens and herbivores and their frequent co-occurrence on the same plants, an understanding of pathogen–insect–plant interactions is then crucial for our understanding of terrestrial plant-based communities.

While the studies to date are convincing, we argue that we have only seen the first glimpse of the potential effects of a community perspective on pathogen–plant–insect interactions. Therefore, we urge more researchers to place pathogen–insect–plant interactions within a community context and be explicit about the spatial and temporal scale of the interactions. With such an approach, we can further unravel the bewildering array of mechanisms and interaction types within cross-kingdom interactions and reveal generalizations across study systems. Here, we point out several promising and largely unexplored directions within the field of three-way interactions, where we focus on the following: (i) the study of cross-kingdom interactions from the perspective of each of the community members, (ii) extend the spatial scale across the soil horizon, (iii) link ecology and evolution in pathogen–plant–insect interactions, (iv) take into account the impact of environmental heterogeneity on pathogen–plant–insect interactions and (v) advance a predictive community framework.

IMPACT OF HERBIVORES ON PATHOGENS

While this review has purposely focused on the impact of pathogens on herbivores, an equal case could be made for the reverse interaction. Indeed, a wide range of papers have shown how herbivores may increase (Leath & Byers 1977; Simon & Hilker 2003), have no effect (Ajlan & Potter 1991, 1992; Rostás & Hilker 2002) or decrease (Karban, Adamchak & Schnathorst 1987; Hatcher *et al.* 1994b; Eyles *et al.* 2007; Yang *et al.* 2011) pathogen infection. Interestingly, while a classical paper by Karban, Adamchak & Schnathorst (1987) showed that the interaction between a pathogen (*Verticillium dahliae*) and herbivore (spider mite) was reciprocal and symmetrical, more recent studies indicate that reciprocity and symmetry may not be the rule (Hatcher *et al.* 1994b; Rostás & Hilker 2002; Simon & Hilker 2003; Eyles *et al.* 2007; but see Rayamajhi *et al.* 2006).

THE SPATIAL SCALE OF PATHOGEN–PLANT–INSECT INTERACTIONS: BEYOND THE SOIL HORIZON

Most attention on spatial variation in pathogen–plant–insect interactions has been limited to interactions involving either plant roots or plant shoots (e.g. Dematheis *et al.* 2012). The past decade has seen an increasing interest in interactions between plant attackers below- and above-ground, and some initial studies have also addressed pathogen–plant–insect interactions in this context (van der Putten *et al.* 2001; Pineda *et al.* 2010). Initial results show that below-ground pathogens may influence above-ground herbivores and vice versa (Bezemer *et al.* 2005; Yang *et al.* 2011). In this context, emerging studies of interactions between below-ground nonpathogenic microbes such as mycorrhizae or plant-growth-promoting rhizobacteria and above-ground herbivores have shown that such interactions are crucial for our understanding of interactions on

either side of the soil horizon (Hartley & Gange 2009; Pineda *et al.* 2010, this issue; Jung *et al.* 2012). Thus, to understand the community ecology of pathogen-plant-insect interactions, it is important to address pathogen-plant-insect interactions across the soil horizon.

FROM ECOLOGY TO EVOLUTION: A COMMUNITY GENETICS FRAMEWORK

The emerging view within community genetics is that intraspecific variation in the community members would affect the ecological and evolutionary community dynamics (Whitham *et al.* 2006; Tack, Johnson & Roslin 2012b). While its relevance in explaining ecological variation is variable (Tack, Johnson & Roslin 2012b), we argue that – as based on strong genotype-by-genotype interactions between plants and pathogens (Thompson & Burdon 1992) – genetic interactions may play an especially important role in structuring pathogen-plant-insect interactions. While few studies have compared multiple pathogen genotypes, some fascinating insights have been gained by two studies using the most extreme interactions types (i.e. compatible and incompatible pathogen strains). These studies show that both compatible and incompatible host–pathogen interactions impact herbivore dynamics, albeit differently (Cui *et al.* 2002; Cardoza & Tumlinson 2006). As an interesting corollary, the impact of incompatible – and often visually absent – infections may often go unnoticed in the field, and field surveys may therefore strongly underestimate the role of pathogen mediation in shaping community structure. In general, pathogen-plant-insect interactions are likely to depend on genetic variation in both pathogens (Cui *et al.* 2002; Cardoza & Tumlinson 2006), plants (Zebitz 1988) and herbivores (Laine 2004). Together these studies indicate that a community genetics perspective may be useful in understanding tripartite interactions.

SPATIAL AND TEMPORAL VARIATION IN THE ENVIRONMENT

Recent studies suggest that spatial and temporal variation in the environment may modify the interaction between pathogens, plants and herbivores. For example, the survival of the European pine sawfly *Neodiprion sertifer* feeding on Austrian pine (*Pinus nigra*) depended on the interaction between fertilization and infection in one of 2 years (Eyles *et al.* 2007). Likewise, the effect of infection of Chinese cabbage leaves by *A. brassicae* on the performance of the herbivorous beetle *Phaedon cochleariae* was affected by the environment: while pupal weight did not differ between infected and healthy leaves when grown at constant temperature (25 °C), pupal weights of beetles reared on fungal-infected leaves under a variable temperature regime (23 °C/12 °C) were reduced as compared to those fed on control leaves (Rostás & Hilker 2002). Moreover, given the dependency of many pathogen species on

both microclimate and regional climatic variation (Schnathorst 1965; Duniway 1979; Burdon 1987), it seems likely that pathogens may be absent in some parts of the landscape. Overall, the environment may impact both pathogen prevalence and interaction outcome, thereby creating selection mosaics and influencing the evolutionary trajectories of the herbivores (Thompson 2005; Biere & Tack, 2013). Focusing on spatial and temporal heterogeneity will then be important to understand the ecology and evolution of pathogen-plant-insect interactions.

TOWARDS A PREDICTIVE COMMUNITY FRAMEWORK

In this article, we explored the intriguing diversity of direct and indirect interactions between plant pathogens and herbivores within a community context. Like in community ecology in general, we are then faced with fascinating but apparently species-specific and complex interactions and the lack of emerging general patterns (Lawton 1999). Nevertheless, we hope that this review will stimulate much-needed studies that may result in a predictive community framework. In particular, we advance two avenues: a genes-to-community and a meta-analytical approach.

In the past two decades, there has been increasing interest in both the ecology of plant-pathogen-herbivore interactions and the underlying mechanisms (Barbosa 1991; Rostás, Simon & Hilker 2003; Stout, Thaler & Thomma 2006). Nevertheless, current studies on mechanisms are frequently conducted in the absence of an ecological context. A key solution is then to integrate studies on a wide variety of topics, like gene expression profiles, signalling and ecological community interactions within the same (preferably natural) study system (Pieterse & Dicke 2007). Here, one promising direction is to explore the different phytohormonal signalling pathways expressed in response to pathogens and herbivores (Pieterse *et al.* 2012; Thaler, Humphrey & Whiteman 2012), where several generalizations have recently emerged. For example, the currently prevailing view states that the SA pathway induces resistance against biotrophic pathogens and some phloem feeders, whereas the JA pathway induces resistance against chewing herbivores, some phloem feeding insects and necrotrophic pathogens. The impact of such guild-specific induced responses in the plant, and the possible trade-offs between the induction of different phytohormonal pathways (Thaler, Humphrey & Whiteman 2012), may then provide a predictive framework for pathogen–herbivore interactions. Another promising direction is to conduct directed manipulative studies by, for example, eliminating or attenuating specific phytohormonal pathways or other phenotypic characteristics and investigate the effects on community ecology (Kessler, Halitschke & Baldwin 2004). By focusing such an approach on variation in the genetic basis and expression of phenotypic characteristics (Zheng & Dicke 2008; Schuman *et al.* 2009; Kloth *et al.* 2012), we may simultaneously gain insight in the raw material of natural selection in tripartite interactions. Overall, we hope

that the further integration of studies on pathogen recognition through signalling pathways, gene expression, and plant metabolic and physiological changes to effects of pathogens on herbivores and the entire multitrophic community will create a mechanistic understanding of the plant food web and herbivore community dynamics.

While the qualitative nature of the current synthesis provides an opportunity to discuss the full scope of direct and indirect interactions within a community context, we hope that our synthesis – and the current special issue on plant-microbe-insect interactions in general – will spur a large enough number of studies to allow for a future meta-analytical review. Notably, such a large body of literature is needed to accurately distil the patterns from the exceptions, as our synthesis suggests that pathogen-plant-insect interactions are highly variable, where each general pattern is counteracted by at least one contradictory example (see also Barbosa 1991; Stout, Thaler & Thomma 2006). Given this high variability, we feel that advancing universal patterns at this point may be misleading and possibly counterproductive. As an alternative, we advance several important questions and hypotheses that could be addressed in future studies and quantitative syntheses:

1. When do we expect that pathogens have a strong effect on herbivores? Does pathogen taxon, guild or specialization explain the impact of the pathogen on herbivores? Can we explain such taxa and guild-specific interactions by the host-quality changes they cause or the phytohormonal signalling pathways they elicit? From the herbivore point of view, particular herbivore taxa or guilds (e.g. chewing insects or phloem feeders) may be differently affected by the presence of pathogens. Moreover, there may be differences between specialist and generalist herbivores in their response to pathogens: for example, specialist herbivores may be better able to deal with pathogen-induced plant chemicals (Ali & Agrawal 2012).
2. Does the general correspondence between preference and performance in insect herbivores (Gripengberg *et al.* 2010) remain valid when the herbivore is faced with healthy and pathogen-infected plants and plant tissues? Fascinatingly, a consistent relationship between preference and performance on healthy and pathogen-infected plants and plant tissues would suggest that not only plant quality but also plant-associated plant pathogens form an important evolutionary selective pressure on herbivore preference (Friedli & Bacher 2001; Röder, Rahier & Naisbit 2007; Tack, Gripengberg & Roslin 2012a; Biere & Tack, this issue).
3. What is the spatial and temporal extent and strength of pathogen-plant-insect interactions? For example, interactions between pathogens and insects may be stronger at the local than systemic scale (Stout, Thaler & Thomma 2006). Moreover, while fine-scale patterns of grazing have been detected (at the scale of millimetres), future studies may probe whether pathogen-induced volatiles may result in the induction of responses in

neighbouring plant individuals. Likewise, the temporal pattern of pathogen induction may play a major role in pathogen-plant-insect interactions, ranging from significant effects within hours to multiple years (and possibly across plant generations; Ali & Agrawal 2012). Hence, the question emerges whether particular pathogen taxa or guilds create distinct temporal patterns? Notably, as induction profiles frequently vary between local and systemic leaves in the rate of development (where the most rapid response generally is locally), herbivores will frequently be confronted with spatiotemporally variable mosaics of pathogen-induced plant quality.

4. Finally, is there a consistent difference in the herbivore response when it vectors the pathogen in question? Are such potentially co-evolving pathogen species more likely to positively affect herbivore performance or preference? Or, as several studies suggest, have they evolved to manipulate the herbivore behaviour to their own benefit (Ferreres & Moreno 2009; Mauck, De Moraes & Mescher 2010; Bosque-Pérez & Eigenbrode 2011; Mann *et al.* 2012; McMenemy *et al.* 2012; Shapiro *et al.* 2012)?

In nature, plants are exposed to a wide range of attackers that include plant pathogens and insect herbivores. By addressing tripartite interactions between plants, insects and plant pathogens and gaining insight in general patterns of such interactions, we will not only improve our knowledge on the ecology and evolution of plant-pathogen-insect interactions in nature, but we may also be able to design durable ways to integrate the management of plant pathogens and insect herbivores in agroecosystems.

Acknowledgements

We thank Tomas Roslin and two anonymous reviewers for constructive comments on an earlier version of the manuscript. The work of MD as part of the European Science Foundation EUROCORES Programme EuroVOL was supported from funds by the Earth and Life Sciences Council of the Netherlands Organisation for Scientific Research.

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Received 14 June 2012; accepted 13 February 2013

Handling Editor: Alison Bennett