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Towards a phylogenetic ecology of plant pests and pathogens

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Plant–pathogens and insect pests, hereafter pests, play an important role in structuring ecological communities, yet both native and introduced pests impose significant pressure on wild and managed systems, and pose a threat to food security. Global changes in climate and land use, and transportation of plants and pests around the globe are likely to further increase the range, frequency and severity of pest outbreaks in the future. Thus, there is a critical need to expand on current ecological theory to address these challenges. Here, we outline a phylogenetic framework for the study of plant and pest interactions. In plants, a growing body of work has suggested that evolutionary relatedness, phylogeny, strongly structures plant-pest associations—from pest host breadths and impacts, to their establishment and spread in new regions. Understanding the phylogenetic dimensions of plant-pest associations will help to inform models of invasive species spread, disease and pest risk in crops, and emerging pest outbreaks in native plant communities—which will have important implications for protecting food security and biodiversity into the future.

This article is part of the theme issue 'Infectious disease macroecology: parasite diversity and dynamics across the globe'.

1. Background

Plant–pathogens and insect pests (hereafter pests) are responsible for major agricultural losses with significant economic and social impacts, while non-native and invasive pests pose additional threats to native plant flora. The Irish potato famine of 1845–1852, sometimes referred to as the Great Famine and perhaps the greatest historically recent societal disruption caused by a plant pest, was estimated to have led to the death of one million people, and the forced migration of up to another two million [1]. The cause of the famine, *Phytophthora infestans*, an oomycete pathogen, has since spread around the globe and remains a serious crop pest of Solanaceae today [2,3]. Likewise, the Great French Wine Blight of the mid-nineteenth century almost ended wine production in France, and was a result of the accidental introduction of the grape phylloxera (*Daktulosphaira vitifoliae*) from North America [4]. The wine industry in France and much of Europe was only saved by grafting winegrape vines to native American *Vitis* rootstock that was resistant to the phylloxera [5].

Plant pests have also contributed to a restructuring of natural plant communities around the globe, reducing the abundance of host plants and, in severe cases, extirpating species from parts of their historic native ranges. *Cryphonectria parasitica*, for instance, causal agent of Chestnut blight, effectively eliminated mature American chestnut (*Castanea dentata*) from its range in North America during the twentieth century [6]. The blight not only contributed to a transition to oak/hickory forests in the Appalachian Mountains, but is also reported to have resulted in the extirpation of multiple moth species and declines in wildlife populations dependent on the chestnuts for food [7]. More recently, sudden oak death and emerald ash borer are having equally consequential impacts on

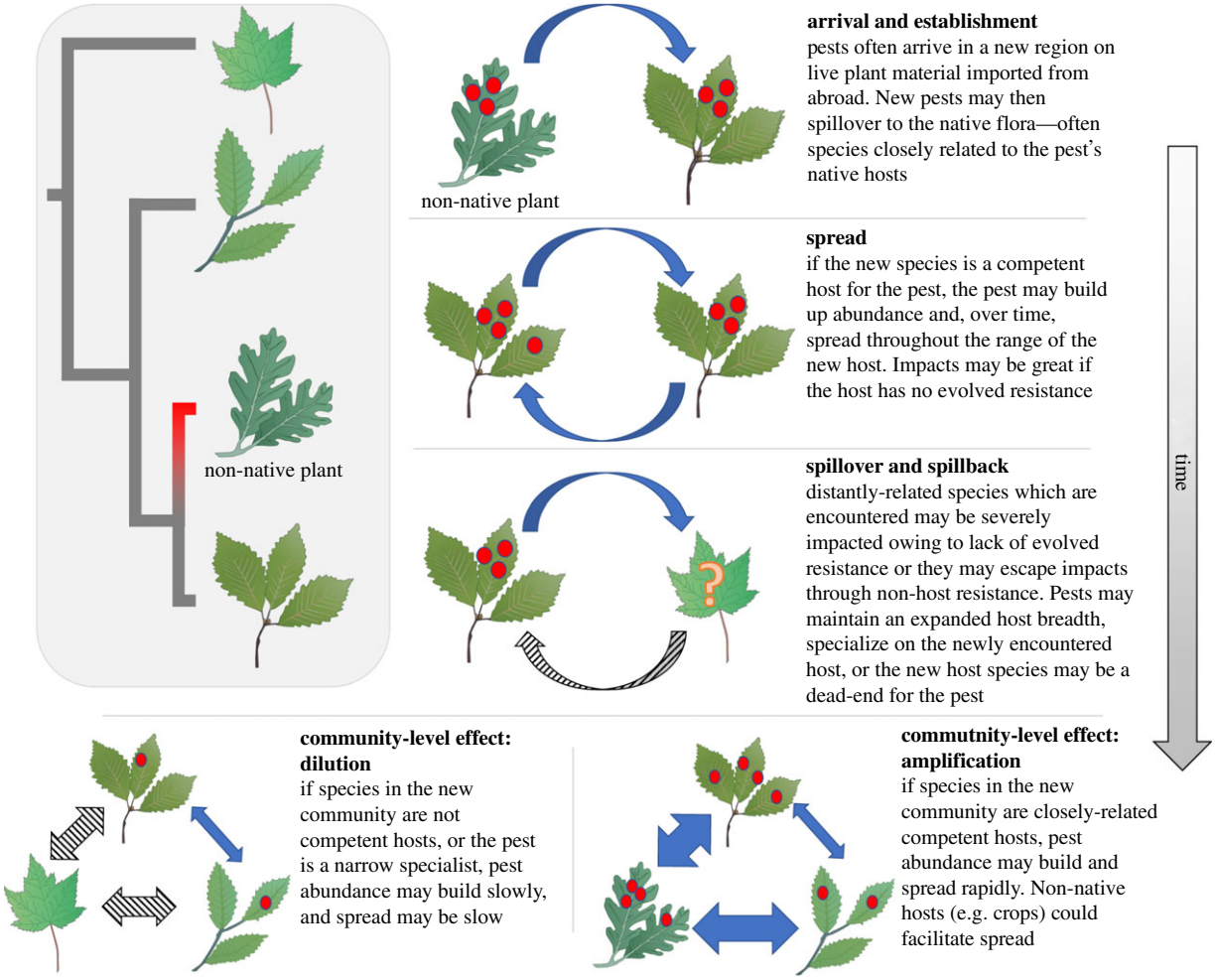

Figure 1. Phylogenetic constraints on the emergence and spread of plant pests introduced to a new region on a non-native plant. Solid red spots indicate pest occurrence on hosts; solid blue arrows indicate transmission between hosts with arrow size proportional to the level of transmissibility; hatched arrows indicate lack of transmission. Leaf images are courtesy of the *T. Saxby*, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). (Online version in colour.)

tanoaks (*Notholithocarpus densiflorus*) and ash (*Fraxinus* spp.), respectively, in North America [8,9].

The recent and historical movement of plants and pests around the globe, both deliberate and accidental, has reshaped plant-pest biogeography and provided numerous opportunities for novel pest-plant associations. While geographical barriers to pest spread have been reduced [10], a growing body of literature indicates that the distribution of pests on host plants retains the fingerprint of evolutionary processes operating over deep time [11–15]. Here, we explore the imprint of evolutionary history on present-day plant-pest associations across the globe, and present a phylogenetic framework for understanding and modelling plant-pest interactions (figure 1). We discuss the role phylogenetic relationships have on pest host breadths, the damage pests cause to hosts, and how the phylogenetic composition of communities may play a role in pest emergence and spread. We conclude by highlighting some of the remaining challenges and opportunities in using phylogenies to improve our understanding of plant-pest interactions.

2. Phylogenetic conservatism in pest-host associations

The taxonomic breadth of host plants that pests can use varies widely—some are known on only one or a few host species (e.g. many rust fungi and gall-forming insects), while others use hundreds or thousands of plant species (e.g. *Rhizobium radiobacter*, bacterial causal agent of a root gall or *Coccus hesperidum*, brown soft scale). While pest attributes are probably important in aligning pests along the specialism-generalism spectrum, for example, viruses are frequently among those with the narrowest host range [16], most pests tend to demonstrate strong phylogenetic conservatism in the hosts they use (e.g. [12,17,18]).

We typically quantify phylogenetic signal on the phylogenetic tree of the focal species, for example, with reference to the evolution of traits along the branches of the phylogeny assuming Brownian motion (see [19]). However, there are two phylogenetic axes that describe pest-host associations [20,21], which may map to different, although not necessarily independent, processes [22]. First, pests may use a phylogenetic subset of hosts, such that closely related hosts tend to be vulnerable to infestation from the same pests. Second, closely related pests may use the same suite of hosts, irrespective of host phylogenetic relationships [23]. In the former, phylogenetic conservatism may reflect evolutionarily conserved pest defence traits among hosts—in this case phylogenetic signal should be quantified on the host phylogeny. In the latter, phylogenetic conservatism may reflect evolutionarily conserved traits of pests that allow them to overcome particular plant defences or identify suitable hosts—in

this case phylogenetic signal should be quantified on the pest phylogeny.

Apparent phylogenetic conservatism on host or pest phylogenies may also arise through shared biogeography, as hosts within any one region will be exposed to the same pest communities [24,25]. For example, if the radiation of host plants has been geographically limited, closely related hosts may share more similar pest communities compared to other regions, not because of intrinsic constraints to pests' host breadth, but rather because of the geographical opportunity for pest-host interactions (see [26] for an example in an insect parasite system). Similarly, indirect phylogenetic conservatism in host breadth might arise if hosts or pests demonstrate phylogenetic niche conservatism (see [27]) in their climatic preferences, such that they are restricted to ancestral climatic niches despite opportunity to spread elsewhere. In these latter contexts, phylogenetic conservatism may be better regarded as a pattern derived from geographical or climatic limitations of pest or host ranges, rather than an evolutionary process that directly operates on host and pest associations (see discussion on the definition of niche conservatism in [28,29]).

(a) Co-diversification of plants and pests

A history of co-diversification can give rise to conservatism along both pest and host phylogenetic axes, assuming host shifts are infrequent or phylogenetically constrained. Co-diversification may arise via shared vicariance, where populations of both hosts and pests become isolated, and through vertical transmission of specialist pests, phylogenetic tracking or coevolution (see perspective by [30]). Because plants and their pests are often thought to be in an evolutionary arms race, we might expect this to lead to increasing specialization of pests over time [31], which could drive diversification of both pests and hosts through ecological speciation [32,33]. Indeed, insect herbivores have been suggested as a major driving force in the evolutionary radiation of angiosperms (see review by [34]). However, pests that are able to use multiple hosts may have a demographic advantage, and thus there could be equally strong selection for wide host breadth within some pests—evident by several of the most damaging and widespread plant pests having extremely broad host ranges (e.g. *Pratylenchus penetrans*, root lesion nematode; *Ceratitis capitata*, Mediterranean fruit fly). The interaction between these two evolutionary forces may help explain some of the large variation in the host breadth of pests we observe today.

(b) Inferences from co-phylogenies

To date, a greater body of research has focussed on the phylogenetic conservatism of hosts used by individual pests, in part, because our knowledge of host plant phylogeny is generally better than our knowledge of pest phylogenies. There are now multiple mega-phylogenies for plants that include tens of thousands of species (e.g. [35,36]) and established approaches for integrating unsampled species using taxonomy (e.g. Phylomatic [37], and more recently V.PhyloMaker [38]) that allow us to reconstruct complete, if less resolved, plant phylogenies for hundreds of thousands of species. Phylogenies for plant pests are, by contrast, less common, typically constrained to one or a few pest genera, and rarely dated. Nonetheless, pest phylogenies are available for some groups (e.g. *Agrilus* [39]; *Phytophthora* [40]) and when combined with phylogenies for plant hosts, allow us to explore both axes of pest-host phylogenetic conservatism simultaneously [23].

Here, as a case study, we examined the phylogeny of the potato blight clade, *Phytophthora* [40], an important group of plant pathogens of agricultural and wild species [41], in relation to the phylogeny of their host plants (figure 2, see the electronic supplementary material, Methods). Closely related *Phytophthora* spp. vary surprisingly widely in their host breadths. While some *Phytophthora* spp. are known on only one or a few closely related plant species (e.g. *Phytophthora brassicae*, *Phytophthora mexicana*), others (e.g. *Phytophthora ramorum*, *Phytophthora nicotianae*) infect plant hosts across the vascular plant tree of life—including ferns, gymnosperms, and angiosperms. Previous work on *Phytophthora* has found growth rate, desiccation resistance, and time since description to be important predictors of the number of host families *Phytophthora* species can infect [43]. We propose that host breadth could also be affected by the diversity of plant tissues the pathogens can attack (figure 3; see the electronic supplementary material, Methods). *Phytophthora nicotianae*, for instance, is known to produce lesions and cankers on roots, stems, leaves and fruit of its dozens of host species. Indeed, among 19 *Phytophthora* species with available data, we found a positive relationship between the phylogenetic diversity of hosts, and the number of plant tissues attacked. The ability to infect multiple tissue types may be an additional important, though unexplored, promoter of host range expansion.

3. Phylogenetic constraints on pest impacts

While there is relatively strong evidence that many pest host ranges are phylogenetically circumscribed (e.g. [12,17,44]), it is less well-established whether the impacts pests have on hosts are similarly structured. Many plant traits involved in pest defence, susceptibility, or apparency (e.g. resin or phenolics production, leaf cuticle thickness, phenology), are phylogenetically conserved (e.g. [45,46]), which could result in closely related hosts being similarly impacted by particular pests. Gilbert *et al*. [47], for instance, showed that the phylogenetic pattern of pest impacts closely matched that of pest host ranges, suggesting similar mechanisms may control pest host ranges and impacts. Additional evidence supporting a phylogenetic signal in pest impacts comes from studies of non-native plants. For instance, Pearse & Hipp [46] assessed leaf damage on 57 non-native oaks in a botanical garden in California, and showed that as phylogenetic distance increased from their native host, *Quercus lobata*, leaf damage tended to decrease—presumably owing to specialized pests of *Q. lobata* being less competent on more distantly related oaks. Other examples of phylogenetic conservatism in pest impacts among non-native plants have been found in plants grown in a common garden in Ontario, Canada, [48] and non-native oaks in Spain [49]. Phylogenetic conservatism in pest impacts is also detectable in native plants. In an analysis of severity ratings of the most damaging pests of North American trees from Potter *et al*. [50], we show (see the electronic supplementary material, Methods) that pest severity tends to decline with increased phylogenetic distance from the most severely impacted host (figure 4). The relationship between evolutionary distance and pest severity, however,

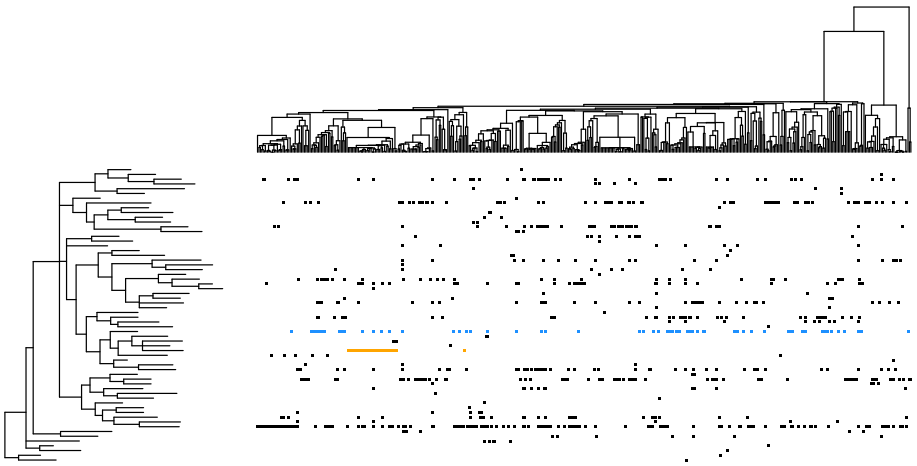

Figure 2. Associations (black squares) between 62 *Phytophthora* species (rows) and 461 plant host species (columns), with their respective phylogenies in the margins—see the electronic supplementary material, Methods. *Phytophthora* species show wide variety in their host breadths, where some are known on just a single host, others are phylogenetic specialists (e.g. *Phytophthora infestans*, orange symbols), and others have hosts widely dispersed across the host phylogeny (e.g. *Phytophthora nicotianae*, blue symbols). The distribution of hosts across the pest phylogeny is equally mixed, with some hosts infested by just a single *Phytophthora* species, while others appear to be susceptible to multiple *Phytophthora* species. *Phytophthora* phylogeny is from Yang *et al*. [40] pruned to include one isolate per species. The plant phylogeny was generated with V.PhyloMaker [38], and pest-host associations are from the CABI Crop Protection Compendium [42]. (Online version in colour.)

also varies between insects and fungi, and whether pests are native or invasive. In general, impact decayed most rapidly with phylogenetic distance for invasive fungi and invasive insects, followed by native insects, and native fungi (table 1 and figure 4).

While the defence traits and underlying genes conferring resistance are often phylogenetically conserved, geography and coevolution between plants and pests may obscure phylogenetic patterns in pest impacts. The importance of biogeography on pest impacts is evident by the disparate impacts of non-native pests in their native and invasive ranges. Often, impacts of pests in their native range are minor, perhaps reflecting the coevolutionary history between pest (virulence) and host (resistance). When introduced to a new region with species closely related to the native hosts, impacts may be far greater, as hosts may have no evolved resistance to the pest, and non-native pests may be released from their own natural enemies or abiotic constraints, allowing higher population levels and larger outbreaks, leading to more damage to hosts (e.g. [51]). Examples are plentiful among invasive pests. Emerald ash borer (*Agrilus planipennis*), for instance, which is currently eliminating *Fraxinus* species in North America is only a nuisance pest in its native range in eastern Asia, despite (mostly) specializing on *Fraxinus* in both its native and non-native ranges [51]. Thus, although host jumps (ecological expansion of pests' host range through infestation of novel host species) or host switching (pests' switching from one host to another via evolutionary changes) may not be particularly (phylogenetically) large, there can be significant disparity in pest impacts on closely related native and non-native hosts—breaking the link between pest impact and host relatedness.

Phylogenetic conservatism in pest impacts could also become obscured following large phylogenetic host jumps. While recent host jumps can be difficult to discern when pests and hosts have not been historically separated (host jumps during invasions tend to be more apparent), the impacts of such host jumps can mirror those of invasions, where novel hosts tend to be more severely impacted—although these patterns have been less frequently documented. In mammals, Farrell & Davies [52], found domesticated host mortality tended to be greater in hosts that were more distantly related to known wildlife hosts, potentially an example of maladaptive virulence—whereby rapid host mortality could impede future pathogen transmission. It is unclear if a similar mechanism is generalizable in plant systems.

4. Pest and plant introductions

(a) Non-native pest establishment and invasion

Phylogenetic conservatism in pests' host ranges suggests that the distribution of pests may be primarily determined by the phylogenetic composition of host communities. Floras in which constituent species are phylogenetically close to pest coevolved hosts are thus more likely to support pest populations as they may provide additional resources to pests, even if they have evolved in isolation. Phylogenetic similarity among host communities might reflect functional or physiological similarity, probably important in pests' host preferences [53], especially if pests have particular diet/resource requirements or if pests use specific olfactory, visual, or chemical cues [54] to detect suitable hosts. Climatic and geographical barriers to dispersal are probably to still constrain pest distributions, but in the former, effects of climate may be mediated through the distribution of hosts, and in the latter, human mediated dispersal (of both hosts and pests) is providing new opportunities for pest spread. Because invasive pests are more likely to establish and spread rapidly in plant communities more closely related to the native hosts of a pest [55], we can estimate the likelihood of pest establishment from the phylogenetic composition of the host community. Gilbert *et al*. [11] present a formal model of this relationship for phytosanitary risk assessment, using the shape of the curve describing the association between the phylogenetic distance separating hosts and the probability of sharing a pest. Given information on the phylogenetic relationships of a recipient flora, the risk of accidental

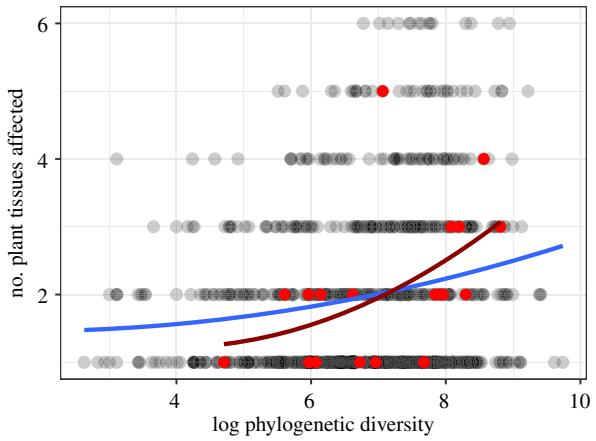

Figure 3. Relationship between the number of plant tissues affected by plant pests and the phylogenetic diversity of their hosts. Plant tissues (i.e. roots, stems, leaves, growing point, inflorescence, fruits, seeds) only include those that are directly impacted by the pest, via production of lesions, mycelium/spores, necrosis, galls or direct feeding on the tissue. Black symbols represent all included plant pests ($n = 922$). Red symbols highlight *Phytophthora* species (with available tissue data, $n = 19$) shown in the phylogeny in figure 2. Lines show fit of a quadratic regression for all pests (less steep blue line) and *Phytophthora* species (steeper red line)—see the electronic supplementary material, Methods. Both regression lines show a positive relationship between phylogenetic diversity and the number of tissues affected, but we note the pests that affect the largest number of plant tissues—across all pests and just *Phytophthora*—have intermediate levels of host phylogenetic diversity. (Online version in colour.)

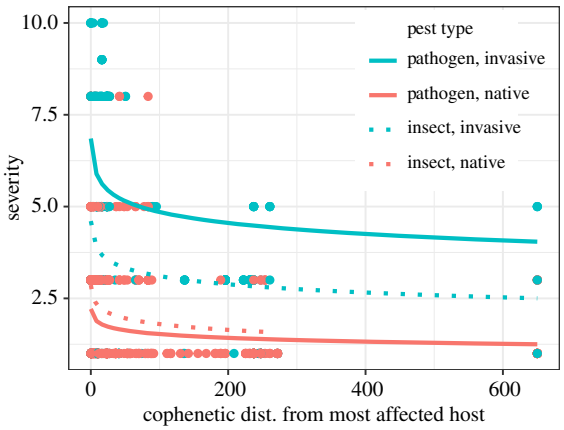

Figure 4. Severity of native and non-native pests on native North American tree species, in relation to the phylogenetic distance from the most severely affected host. Lines show best fit regressions modelled as severity $\sim b_0 + b_1 \times \log_{10}$ (cophenetic distance + 1), for each combination of pest type (pathogen and insect) and nativity (native and invasive)—see the electronic supplementary material, Methods. Note the impacts of invasive pests tend to be higher and decay more rapidly with cophenetic distance than native pests. The gap between approximately 275–650 reflects the large phylogenetic distance that separates angiosperms and gymnosperms. Severity ratings are from Potter *et al.* [50]. See table 1 for model coefficients. (Online version in colour.)

introduction of a novel pest with the deliberate introduction of a non-native plant, e.g. for horticulture, can then be quantified. Put simply, non-native plants that are closely related to recipient floras will be more likely to pose high risk of introducing novel pests to which the native flora may be susceptible.

Phylogenetic conservatism in host preferences and impacts also provides valuable information on assessing pest risks for biosecurity, especially when the complete host range of a particular pest is not known. For example, if a given pest (native or non-native) is known to use the native flora of a region, then close relatives of that pest may also pose a threat. Indeed, many non-native conifer-specialist insects in North America, for instance, are known to have native congeners [56]. Furthermore, some pest taxa are already widely recognized as general threats to agricultural crops and native floras, for example, fruit flies (*Drosophila*), tussock moths (e.g. genera *Orgyia* and *Lymantria*), leaf roller moths (family Tortricidae) and thrips (order Thysanoptera) (see [57] and references therein). Using phylogenetic distance rather than crude taxonomy would provide more fine-scale risk assessments, and could be easily extended to other pest groups which have been less intensively studied but which could prove to be future threats.

(b) Introducing pests for biocontrol

While most non-native plant pests are introduced accidentally, some pests are introduced intentionally as biocontrol agents. Phylogenetic conservatism in host preferences and impacts can similarly inform selection of both biocontrol agents and suitable target hosts. A major risk in biocontrol is host switching from the intended target to native, non-target species [58]. It has long been recognized that non-target hosts that are most vulnerable are those most closely related to the target species (see e.g. [59])—good targets for biocontrol are thus weeds with few or no close relatives in the native flora [59]. If the intended target is a non-native weed, it is common practice to introduce a pest from the target's native range [60]; however, if the pest has close relatives that use plants in the target's non-native range, then this might indicate a high risk of spillover. A good biocontrol agent is thus a pest that infests the weed in its native range, but which has few close relatives in the invaded range.

While host specificity is a major factor in selecting biocontrol agents, some pests may appear highly host specific because geographical barriers have limited opportunity for host range expansion. It is not uncommon to discover that apparent specialists may opportunistically jump to new hosts when introduced in a new geographical region [61]. It is obviously impractical to challenge prospective agents against all possible native hosts, nonetheless, we may be able to learn from the pest phylogeny. Pest within clades demonstrating strong phylogenetic signal in host affinity may be less likely to spill over to non-target hosts, whereas pests within clades where host affinity is highly labile might represent high risk to the native flora if introduced. An optimal scenario for biocontrol is thus a target weed with no close relatives in the native flora, and a control agent with narrow phylogenetic host range, nested within a clade with high phylogenetic conservatism in host affinities, and with no close relatives that use the native flora.

(c) Plant introductions and the enemy release hypothesis

One explanation for why some plants are able to successfully establish and invade regions outside their native range is that they may experience an ecological advantage through escaping the pests in their native distribution—the enemy

Table 1. Regression coefficients for models of pest impacts on North American trees as a function of cophenetic distance from the most severely impacted host. (Models were fit as severity $\sim b_0 + b_1 \times \log_{10}$ (cophenetic distance + 1). See figure 4 for model fits.)

pest type	nativity	*n*	intercept	slope
disease	invasive	122	6.853	−0.998
disease	native	464	2.213	−0.342
insect	invasive	222	4.606	−0.748
insect	native	292	2.865	−0.531

release hypothesis (see [62]). While there is some strong evidence in support of enemy release, the mean effect size might not be large [63,64], only a small proportion of introduced species go on to become invasive (e.g. [65]), and many non-native plants accumulate pests over time [66]. Introduced plants may bring their pests with them, or native pests may jump to the non-native plant—either of which could mean that non-native plants do not experience the full demographic benefits of enemy release. However, if pests' host preferences are phylogenetically constrained, then non-native species more phylogenetically distant from the native plant community may be less susceptible to native pests, and therefore more likely to experience benefits of enemy release (assuming hosts do not bring their own pests with them).

While there is as yet no consensus on whether phylogenetically distinct species are better able to invade native communities [67,68], growing evidence suggests this might reflect, at least to some extent, difference in the spatial and phylogenetic scales assessed [69,70]. At local scales, where biotic interactions probably play an important role in community assembly, a number of recent studies have found non-native plant species tend to be phylogenetically distinct from the native flora [71–73]. The observation that non-native species with few close relatives are better able to establish when introduced into novel communities was perhaps first noted by Charles Darwin. In what is now commonly referred to as Darwin's naturalization hypothesis, Darwin hypothesized that resource-use overlap, and thus competition with native species, would be lower if introduced species were more distant relatives. Both Darwin's naturalization hypothesis and the enemy release hypothesis predict similar ecophylogenetic patterns [74], such that additional information is needed to differentiate between them. However, because pests of non-native plants may over time invade the introduced range of the non-native plant, and pests of the native flora can evolve to use novel hosts (both commonly observed in intentionally introduced plants e.g. [75,76]), testing for evidence of enemy release may require catching the pest-free window of opportunity that allows non-native species to establish a foothold in native plant communities [77].

5. Pest prevalence and emerging pest outbreaks

(a) Dilution and amplification

The phylogenetic conservatism in pest host breadths has major implications for the relationship between host diversity and disease prevalence—the dilution/amplification effect of diversity on pathogens—and host species coexistence. There has been much recent debate on whether host diversity acts to dilute disease pressure [78]. Perhaps the most well-cited example is the decrease in the prevalence of Lyme disease (caused by the bacterium *Borrelia burgdorferi* and vectored by the black legged tick, *Ixodes scapularis*), in species rich animal communities [79]. In species poor communities in North America, the white footed mouse, *Peromyscus leucopus*, tends to dominate host communities. As the mouse is a competent host for both tick and bacterium, Lyme disease prevalence also tends to be greater in such communities. In more diverse communities, less competent hosts are more frequently encountered by the tick and, as a consequence, prevalence of Lyme disease is lower. However, support for the dilution effect is mixed, and in some instances increased host diversity has been associated with greater disease prevalence, for example, owing to pathogen spillover [80]. While the dilution effect in plants has been less well studied, there appears to be significant support for dilution effects of diversity on aggregate, but large variation across systems (see [81]).

The mechanisms for the dilution effect in plants are suggested to include the physical interception of spores or vectors by non-host species [82], and the reduction of competent host abundance [83]. It is not clear, however, why increasing diversity should amplify disease in one system, but dilute disease in another, although some evidence exists that the underlying level of host diversity may affect the strength of amplification and dilution. Guo *et al.* [84], for instance, found a hump-shaped relationship between tree diversity and non-native pest diversity. They suggested that amplification and dilution occur simultaneously in forests but the directionality of the mechanism depends on the initial host diversity (i.e. amplification at low diversity, dilution at high diversity). If this pattern is consistent across spatial scales, it could have important implications for conserving high-diversity communities in order to buffer against establishment of non-native pests.

The phylogenetic composition of host communities provides an alternative explanation for the mixed evidence supporting amplification/dilution effects. As we discuss above, there is evidence to indicate that pests are both constrained in the phylogenetic breadth of hosts they can use and that closely related hosts experience more similar pest impacts. If we assume that pests which are able to feed more and reproduce more rapidly will have higher impact on their hosts, we might then infer that there is a phylogenetic signal in host competence. Thus, host communities composed of closely related taxa are both more likely to share pests, and those pests are likely to increase in prevalence—an amplification effect of diversity on pathogen prevalence. However, host communities composed of less phylogenetically close hosts are less likely to share pests and are more likely to differ in their competence as pest reservoirs. More phylogenetically diverse host communities might thus support a greater diversity of pests (higher pest turnover between hosts), but average pest prevalence will be lower—a dilution effect of (phylogenetic) diversity [85]. Because pests and pathogens also regulate host abundance, the increased pest pressure in less phylogenetically diverse host communities will tend to depress (competent) host abundances, and facilitate invasion by (less competent) hosts that

are phylogenetically distinct. These phylogenetic dilution/amplification effects will therefore tend to shift host communities to increasing phylogenetic diversity—a phylogenetic Janzen-Connell effect [85,86].

(b) Emerging pest outbreaks

Numerous factors may contribute to the emergence of native and non-native pest outbreaks, including agricultural intensification, natural and unintentional expansion of pest geographical ranges, and evolution of new pest genotypes with heightened virulence or expanded pest host breadths [87]. Many recent emergent pests are the result of shifting pest distributions owing to the increased transport of biological material around the globe. Pests, however, are also shifting their ranges naturally, in association with extreme weather events, and in response to recent climate change—by some estimates certain pest types are shifting northwards at rates greater than 5 km yr^{-1}. In addition to shifting ranges, warmer climates may also lead to more favourable conditions for pests, allowing more rapid generation times, and larger pest population sizes that could result in more frequent and severe outbreaks [88]. The stages of pest emergence in novel host populations are probably similar to those for emerging infectious diseases in wildlife. Wolfe *et al.* [89] document the five stages of disease emergence in humans, from initial spillover from a wildlife reservoir (stage 1), through various thresholds of sustained replication in human populations (stages 2–4), and finally emergence of a disease endemic to humans (stage 5). We present here a phylogenetically informed framework for the emergence of plant pests (figure 1).

(c) Agriculture and food security

Many agricultural crops are planted in highly abundant and dense monocultures, and thus represent a resource-rich target for pests. The widespread planting of relatively few crop species outside their native range (thus allowing them the benefit of enemy release), may therefore inadvertently select for the evolution of pest host range expansion (see [90,91]). Native pests that are able to expand their host breadth to use agricultural crops will have a strong selective advantage, even if, *per capita*, native species are more competent reservoirs hosts. While phylogenetic conservatism in pest host breadth is still apparent in crop pests [92], it is possible that the resource advantage provided by agricultural crops is large enough to overcome the phylogenetic distance inhibiting native host range expansion. Furthermore, declines in many native host species [93] mean a shrinking resource pool of native hosts for some pests (e.g. as has been described using metacommunity/metapopulation theory [94,95]). For host specialists, the extirpation (i.e. local extinction) of a host will also commit the pest to local extinction. Indeed, intentional local removal of hosts is often used as a means to contain or eliminate pests [96,97]. For multi-host pests, many hosts might have to be lost before a pest is committed to extinction [98]. However, because of phylogenetically structure in both extinction risks [99] and host preferences of pests, pests that use threatened clades may be at higher risk of extinction than predicted solely from their host breadth.

Pests may remain generalists, and simply expand their host ranges as they infest novel agricultural hosts; however, in some cases, specialization following a host jump may further drive pest emergence on novel hosts [32]. Agricultural practices, such as the application of insecticides and fungicides, provide a strong selective pressure for evolutionary divergence (e.g. in biocide resistance genes; [100]), promoting speciation. Giraud *et al.* [32] suggest a number of pest traits may also facilitate emergence and speciation on a novel host, including the production of a large number of propagules, asexual reproduction, and weak genetic controls on host specificity. This process of host jumps followed by host specialization by the pest is distinct from the evolutionary arms race driving co-diversification. Here, diversification is predominantly one sided. Examples in agricultural settings include the rapid radiation of the pea aphid, *Acyrthosiphon pisum*, on legumes (see citations in [91]), and the ongoing (apparent) speciation of the fall armyworm (*Spodoptera frugiperda*) on different hosts [101].

6. Future challenges and opportunities

Plant host phylogenies and, to a lesser extent, pest phylogenies have improved our understanding of pest host-ranges, their impacts, the emergence of plant pests following host and pest introductions as well as the abundance and distribution of hosts (e.g. via Janzen-Connell effects), and pests (e.g. via amplification/dilution effects). There are, of course, limitations to using phylogenies as a proxy for the resistance and virulence traits underlying these patterns. Trait differences among host/pest taxa, for instance, probably do not match perfectly to phylogenetic distances [102]. The lack of concordance between traits and phylogeny probably contribute to the variability in host ranges, whereby some pests appear unconstrained by phylogeny, while others are limited to a narrow group of closely related species. The ability to infect or feed on multiple plant tissues could also play a role on pest host ranges, as we have suggested here, but more work is needed to understand the mechanisms underlying this pattern.

There is also a critical need for better pest phylogenies, which include global samples and multiple genera. Pest phylogenies will not only help improve our understanding of plant pest evolutionary ecology, but will also provide important information on the relationship between native and invasive pests and their respective impacts. Relatedly, there is a need to integrate plant and pest traits into models of pest impacts, and to understand the link between host breadth and pest impacts (see [52] for an example in domesticated mammals). A better understanding of these interrelationships will help to identify impactful pests that may be most at risk of invasion. Identifying potential future invasive pests is an ever more pressing concern given the increasing movement of plants and pests around the globe and climate change driven range shifts that present opportunities for novel pest-host associations (Morales-Castilla *et al.* [103]) in communities with no contemporary analogs [104].

Data accessibility. This article has no additional data.

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