

LETTER

Host phylogenetic diversity predicts the global extent and composition of tree pests

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Editor: Christoph Scherber**Abstract**

Tree pests cause billions of dollars of damage annually; yet, we know little about what limits their regional composition and distribution. Here, we model the co-occurrence of 4510 pests and 981 tree host genera spread across 233 countries. We show the composition of tree pests is primarily driven by the phylogenetic composition of host trees, whereas effects of climate and geography tend to be more minor. Pests that utilise many hosts tend to be more widespread; however, most pests do not fill the geographic range of their hosts—indicating that many pests could expand their extents if able to overcome barriers limiting their current distribution. Our results suggest that the establishment of pests in new regions may be largely dictated by the presence of suitable host trees, but more work is needed to fully understand the influences climate has on the distributions of individual pest species.

KEYWORDS

biogeography, geographic distributions, host breadth, phylogenetic diversity, tree insects and diseases

INTRODUCTION

Plant pathogens and insect pests (hereafter, pests) cause billions of dollars of damage to crops and forests annually that poses a threat to food and economic security (Pimentel et al., 2001; Strange & Scott, 2005), and global biodiversity. In North America alone, non-native tree pests cause over \$4.2B in economic losses annually and have resulted in the near and/or ongoing extirpation of multiple native tree taxa (e.g., *Castanea dentata* from chestnut blight, and *Fraxinus* from emerald ash borer). Native plant pests, however, are an important component of forest ecosystems. In addition to providing crucial ecosystem services, such as decomposing woody material and facilitating forest regeneration, native pests may maintain plant diversity and contribute to biodiversity gradients by limiting the local abundance and distribution of host plants (Bever et al., 2015; Schemske et al., 2009).

Despite their importance to agricultural and natural systems, relatively little is known about the global drivers

of the extent and composition of tree pests, especially compared to their free-living tree hosts (Keil & Chase, 2019). While pests and parasites, in general, have often been found to follow many of the macroecological ‘rules’ observed in free-living organisms (e.g., species area relationship, latitudinal diversity gradients; Stephens et al., 2016), their reliance on hosts for sustenance and reproduction presents a challenge to conceptual frameworks that emphasise the importance of climate at broad scales, and biotic effects at local scales (Peterson, 2008).

Here we consider the effects of climate, geography and host availability on regional pest compositions. These three axes represent major mechanisms potentially impacting pest compositions via environmental filtering, dispersal limitations, and host-pest interactions, respectively. While pests’ reliance on hosts clearly contributes to their local distributions, it is unclear if biotic interactions with hosts are reflected at macroscales, or whether pest distributions are dominated by climate and geography, similar to their free-living hosts. A strong influence of host availability would likely result in a similar

bioregionalisation of host and pest compositions, perhaps reflecting biogeographic regions where pests and hosts have interacted over extended periods of time. The influence of climate, geography, and host availability, which may vary geographically, do not act in isolation and their combined effects likely limit the distribution of individual pests to only a small proportion of their potential ranges.

Climate and geography

Temperature is often recognised as the most important limit on plant distributions and diversity (Huang et al., 2021; McFadden et al., 2019; Wang et al., 2009) and could likewise influence pests either directly by placing thermal limits on pest occurrences, or indirectly by affecting the distribution of host trees. Recent global analyses, for instance, have shown the abundance of soil pathogens is largely driven by temperature (Delgado-Baquerizo et al., 2020), while experimental work frequently shows a strong coupling of environment and pest development (e.g., Faticov et al., 2020). Direct climate influences on pest distributions are also evident from shifting pest ranges in response to recent climate change (Bebber et al., 2013) and climate controls on periodic outbreaks of native pests (Aukema et al., 2008).

In addition to climate, geographic constraints may also limit pest distributions. The importance of long-distance dispersal barriers in constraining pest distributions is evidenced by the ability of non-native pests to establish and spread in new regions after crossing barriers that have historically precluded natural dispersal (Garnas et al., 2012; Wilson et al., 2009). The increasing rate of introduction of some pests (Aukema et al., 2010), and the lack of accumulated saturation of non-native species globally (Seebens et al., 2017), suggests many species are capable of expanding their geographic extents. Introduced pests, however, have likely resulted in increasing biotic homogenisation of pest communities (e.g., Bebber et al., 2014), which may obscure the role of geographic barriers on present-day pest compositions.

Host availability and phylogeny

Pests are necessarily limited by the geography of their hosts—biotrophic pests, for instance, cannot occur where hosts are absent (Poulin et al., 2011). Although indirect and direct effects of climate and host availability may be difficult to separate at broad scales, the primacy of host availability is commonly apparent when pests track their hosts outside the native range to regions with novel climates, beyond those experienced in the native range. Forestry trees grown widely outside their native ranges, for instance, have frequently been invaded by pests from their native ranges (Paine et al.,

2011; Wingfield, 1999). Host availability is also important in pest native ranges, where there is often a link between pest and host diversity (Brändle & Brandl, 2001; Liebhold et al., 2018). Hosts of many pests, however, are phylogenetically constrained (e.g., Gilbert et al., 2012; Gilbert & Webb, 2007; Pearse & Altermatt, 2013), which could indicate that phylogenetic regionalisation of host trees across continents may be important to limit the regional compositions of pests. Host phylogeny may be particularly important for microorganisms such as fungi and bacteria which must have the ability to overcome direct exposure to plant defence chemicals (which may be phylogenetically conserved, Carrillo-Gavilán et al. 2015; Pearse & Hipp, 2009) in order to persist on or within host tissue. Endoparasitism may also contribute to the narrower host breadth of many microorganisms compared to free-living arthropod pests (Gilbert et al., 2012). Pests able to persist on a diverse array of hosts, in contrast, may utilise different hosts in different parts of their range, thus occupying a larger geographic extent than specialist pests (e.g., as seen in some mammalian parasites; Krasnov et al., 2005).

Host range filling

Strong, direct effects of either geography or climate in structuring pest compositions could limit the extent that pests fill the distribution of their hosts. If geographic or climatic constraints were reduced, for example, through unintentional assisted long-distance dispersal or in association with environmental change, pests could likely expand their ranges to fill a greater proportion of their hosts' geographic ranges. However, if host geographic ranges are the primary determinant of pest distributions, and pests occupy most of the range of their hosts, pest range expansion will be limited by host geographic extents and conservatism in host breadth. Thus, understanding the primary drivers of pest compositions, and the degree of host range filling, is critical to quantifying the potential for pests to shift their ranges in response to ongoing global change and for protecting the economic and ecological services trees provide.

A global analysis of tree pests

Here, using global datasets of host tree and pest occurrences, we quantify the relative roles of host availability, climate and geography on the global composition of tree pests, and assess the degree to which pests fill their hosts native ranges. While we expect that geographically adjacent regions with similar climates will have similar pest compositions, we predict that host availability will be the most important factor limiting pests distributions. We also evaluate whether host availability is more important for endoparasites (e.g., bacteria, fungi, viruses,

nematodes), which may tend to have narrower host breadths than arthropods (Bebber et al., 2014; Gilbert et al., 2012). We use an index of host range filling to then examine the extent to which the interaction between climate, geography, and host availability may limit pests' abilities to fill host native ranges. We test the prediction that microorganisms are able to fill a larger proportion of their hosts' ranges because of their propensity for large population sizes, and the ability to produce a large number of easily-dispersed propagules (O'Malley, 2007).

MATERIALS AND METHODS

Pest, host, and geographic distribution data

We extracted geographic and host breadth information from the Centre for Agriculture and Bioscience International (CABI) Crop Protection Compendium (CPC) (CABI, 2020), in December 2020. The CPC collects geographic and host information from the literature and national reporting agencies, for thousands of pests damaging to crops and forest trees worldwide. Amongst its sources, the CPC draws on CAB Abstracts which indexes >10 million research records, including publications from over 120 countries and 50 languages. Following the Food and Agriculture Organisation, the CPC defines pests as any species or pathogenic agents injurious to plants or plant products. We selected pests that had both geographic and host breadth information and at least one tree host (see below). We included eight pest types in our analyses, including arthropods, bacteria, chromists, fungi, molluscs, nematodes, protists, viruses and several pests of unknown aetiology.

Country-level tree geographic distributions were obtained from the GlobalTreeSearch (Beech et al., 2017), which maintains a list of native tree species present in each country, compiled from regional and national checklists and eFloras. We downloaded lists for each country named as a host country for any pest in the CPC data. Tree host names were standardised using the GBIF backbone, accessed with the *rgbif* package (Chamberlain & Boettiger, 2017).

To ensure the robustness of our results and evaluate sensitivity to possible incomplete sampling of understudied tree species, we explored host breadth defined at both genus- and species-levels. Many pests affect multiple species within genera, so assessing hosts at the genus level provides a conservative estimate of a pest's host breadth (Gilbert et al., 2012; Novotny & Basset, 2005); while species-level host designations are more precise, they will likely be more greatly impacted by missing host associations. Species-level hosts were identified by matching hosts in the CPC against a list of all tree species from the GlobalTreeSearch. Determining genus-level hosts required multiple steps. First, all species-level hosts were retained, with specific epithet removed. Next,

for hosts in the CPC only defined to the genus-level, we checked these against a list of genera that include only free-living, woody species. This second step was necessary to prevent the inclusion of genera that included multiple growth forms (i.e., that were not trees) when hosts were only defined as genera in the CPC. For instance, if '*Solanum* sp.' was listed as a host in the CPC, it was not included as a genus-level host because, although *Solanum* includes several tree species, it also includes multiple herbaceous agricultural plants. Growth form information and woodiness data were downloaded from Taseski et al. (2019) and Zanne et al. (2014). In total, we assessed 3828 pests associated with 2694 tree species and 4510 pests associated with 981 tree genera in 233 countries. Because results were broadly consistent regardless of host taxonomic resolution, we focus on genus-level hosts in the main text and present species-level results in the Supplement.

Phylogenetic and spatial analyses

We extracted phylogenetic relationships among host trees using V.PhyloMaker (Jin & Qian, 2019). Host genera and species not included in the backbone were added to the basal node of the inclusive family or genus, respectively.

For each pest, we calculated three phylogenetic metrics of host breadth, specifically: phylogenetic diversity, phylogenetic species variability and phylogenetic species richness. Host phylogenetic diversity (PD) was quantified as the sum of phylogenetic branch lengths of all hosts, without including the root (Faith, 1992). Phylogenetic species variability (PSV) is a metric of phylogenetic relatedness, independent of species richness, which varies between 0 (species are closely related) to 1 (species are unrelated) (Helmus et al., 2007). Phylogenetic species richness (PSR) is quantified as species richness multiplied by PSV and can be interpreted as a measure of species richness after accounting for species relatedness (Helmus et al., 2007). Host phylogenetic aggregation was assessed using mean nearest taxon distance (MNTD) and mean pairwise distance (MPD). Both MNTD and MPD were calculated as standard effect sizes based on 999 randomisations of tip labels (Kembel, 2009). Negative values of MNTD and MPD indicate phylogenetic clumping, while positive values indicate phylogenetic dispersion. Phylogenetic metrics were calculated with the *picante* package (Kembel et al., 2010).

Pest geographic extent was quantified as both the number of countries and biogeographic realms where pests and hosts co-occur. Biogeographical realms were included to reduce sampling effects that could emerge from unequal sampling effort among countries and represent large geographic areas with distinct, natural assemblages of species, where hosts and pests may have interacted over long periods of time. The seven biogeographic realms considered include Afrotropical,

Australasia, Indo-Malay, North America, South America, Eurasia, and Oceanic Islands, and were defined using a polygon based on Olson et al. (2001). Countries were considered to belong to the biogeographical realm that their centroid fell within. The relationships between pest geographic extent and host breadth were evaluated using a weighted Pearson's correlation coefficient, where weights were the sum of country areas that pests occupied. Pests with 0 geographic extent—pests only occurring in regions where hosts were not native—were removed from these analyses.

To assess the degree of range filling by pests (i.e., saturation), we calculated the proportion of countries where pests occur relative to the number of countries in which its hosts are present. Geographic saturation can be described using set theory,

$$\text{Saturation pest}_x = \frac{|A \cap B|}{|B|},$$

where A is countries with the pest_x , B is countries with native tree hosts of pest_x . Low saturation indicates pests occupy only a small portion of the countries where hosts are present. The numerator was also used as our metric of country occurrences. We calculated a spatial metric of saturation within realms using the same equation as above but where A is pests within the realm, and B is pests of native trees in the realm. Realm saturation represents the percentage of pests of native trees that occur within the realm, given the native tree hosts.

Pathogen and host assemblages

We used generalised dissimilarity models (GDM) to assess the relationship between pest compositions and the phylogenetic composition of hosts, climate, geographic distances, and country per capita gross domestic product (GDP). GDMs are a type of matrix regression (Ferrier et al., 2007) that can account for the non-linear change of pest compositions along with explanatory variables and have been shown to provide a better fit to parasite compositional change than linear approaches (Mescht et al., 2017). Differences in pest assemblages were quantified using the Jaccard index. For tree host taxa, we calculated phylogenetic beta-diversity using the UniFrac metric, which measures the fraction of unshared branch lengths between host assemblages within countries. Climate variables included the spatial average and standard deviations of mean annual temperature and mean annual precipitation extracted within countries. Mean annual temperature and precipitation were downloaded from WorldClim (bioclimatic variables *bio1* and *bio12*, Fick & Hijmans, 2017) at a resolution of 10 arc-minutes. These four climate variables were only moderately correlated (strongest correlation

among climate variables was between temperature variability and precipitation variability, $r=0.5$). Geographic distance was calculated as the distance between country centroids. We included country GDP to account for potential sampling effects among countries, as could occur if wealthy countries had superior capabilities to diagnose the occurrence of particular microorganisms. Country GDP was downloaded from the CIA factbook (Central Intelligence Agency, 2020). We assessed variable importance in the models by permuting each predictor variable 99 times and assessing the decline in model performance (deviance explained). Models were fit for all pest species in aggregate, and for arthropods, bacteria, chromists, fungi, nematodes, and viruses separately. Separate models were not fit for molluscs and protists as these groups included few pest species (<10 species). Permutations and model fitting were conducted with the *gdm* package (Manion et al. 2017). We also assessed the proportion of pest beta-diversity due to nestedness and turnover, using the *betapart* package (Baselga & Orme, 2012), to quantify the extent to which pest compositional differences could be due to differences in pest richness (nestedness) which may arise through differences in sampling between countries.

Because host and pest compositions could be similar due to coincidental bioregionalisation across continents (as could occur between non-interacting organisms), we used Mantel tests and multiple randomisation schemes to test if the observed similarity in host/pest compositions were stronger than expected by chance. We used three different randomisations that maintained global patterns of regionalisation. First, we randomly selected non-host trees in countries, up to the total richness of hosts, and used the Jaccard index to quantify (non-host) tree composition change between countries. Second, we quantified general tree composition change by randomly selecting trees in countries irrespective of hosts status (i.e. hosts and non-hosts) while maintaining total richness of hosts in countries. Finally, we repeated the second randomisation procedure but using phylogenetic beta-diversity (UniFrac), as in our main analyses described above, rather than the Jaccard index. Each randomisation was run 999 times to generate a null expectation with which the observed test statistic was compared.

RESULTS

Tree pests are strongly aggregated on both the host phylogeny (i.e., closely related hosts share similar pest assemblages; Figure 1) and geographically (i.e., adjacent geographic regions share similar pest assemblages; Figure 2). Although most pests (56.3%) were known on only one host genus (Figure S1), of the pests with more than one host, 86%–90% utilised hosts that were more closely related than random expectations (i.e.,

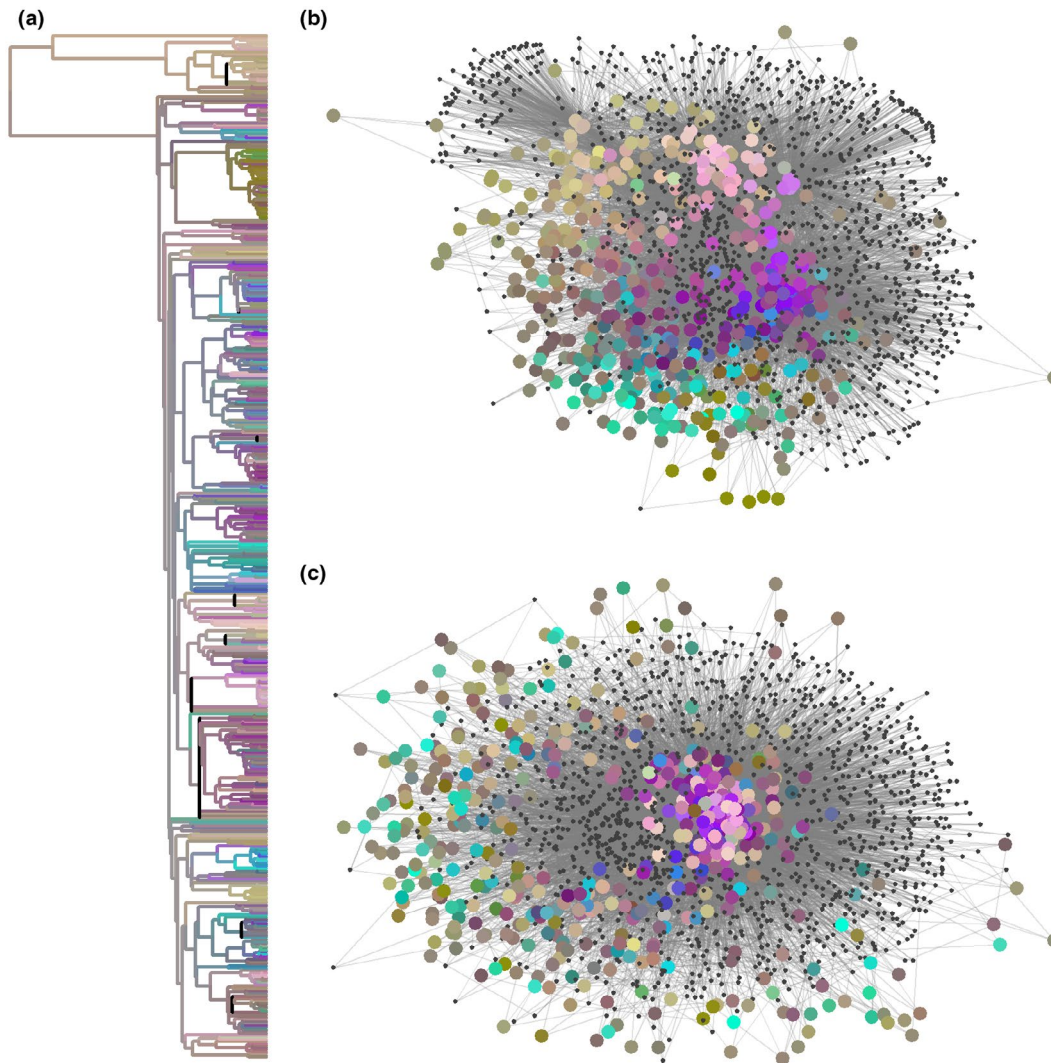


FIGURE 1 (a) Host tree phylogeny, (b) observed host-pest network and (c) randomized host-pest network. Tip colors in (a) and colored circles in (b) and (c) show the compositional similarity of pests among tree genera, and black circles are pests. Colors are based on multidimensional scaling of pairwise pest dissimilarity (Jaccard index) between genera, and assigning the first three axes to the red-green-blue color model. Internal branches were colored by estimating the ancestral state of each red-green-blue intensity individually, and combining them to a single color. Randomized network (c) shows expectations if pests were randomly distributed among hosts while maintaining pest richness within hosts, and connectance within the network (proportion of realized links between pests and hosts, pest-host connectance: 0.02). Genera with more than two pests and pests with more than two hosts were included in this visualization. Color intensities are solely for illustration purposes

standard effect sizes (*ses*) < 0, median *ses* = -0.83 ± 1.51 and -1.32 ± 1.47 , for MPD and MNTD, respectively) (Figure S2), and approximately 40% of pests utilised hosts significantly more closely related than expected by chance (MPD: 40.3% and MNTD: 39.4% of test statistics departing significantly from null expectations at $p < 0.025$). Pest and host compositions were also significantly geographically structured (distance decay in compositional similarity: Mantel = 0.37, $p < 0.01$ and Mantel = 0.53, $p < 0.01$, for the correlation between pest dissimilarity and log geographic distance, and host phylogenetic dissimilarity and log geographic distance, respectively), with nearby countries tending to have more similar pest and host compositions than more distant countries.

Roles of host phylogeny, climate, and geography on pest compositions

Host tree phylogenetic beta-diversity was the strongest predictor of pest compositional dissimilarity for all pests in aggregate and for four of six pest types (arthropods, bacteria, fungi, nematodes; Figures 3, 4, Figures S3, S4). Of the four climate variables assessed, mean temperature was the most important climate variable whether pests were assessed in aggregate or as individual pest types. Geographic distance was not important in explaining compositions of any pest types (Figure 4). Per capita GDP, included to control for possible sampling effects, tended to have low importance for most pest types, except for viruses and

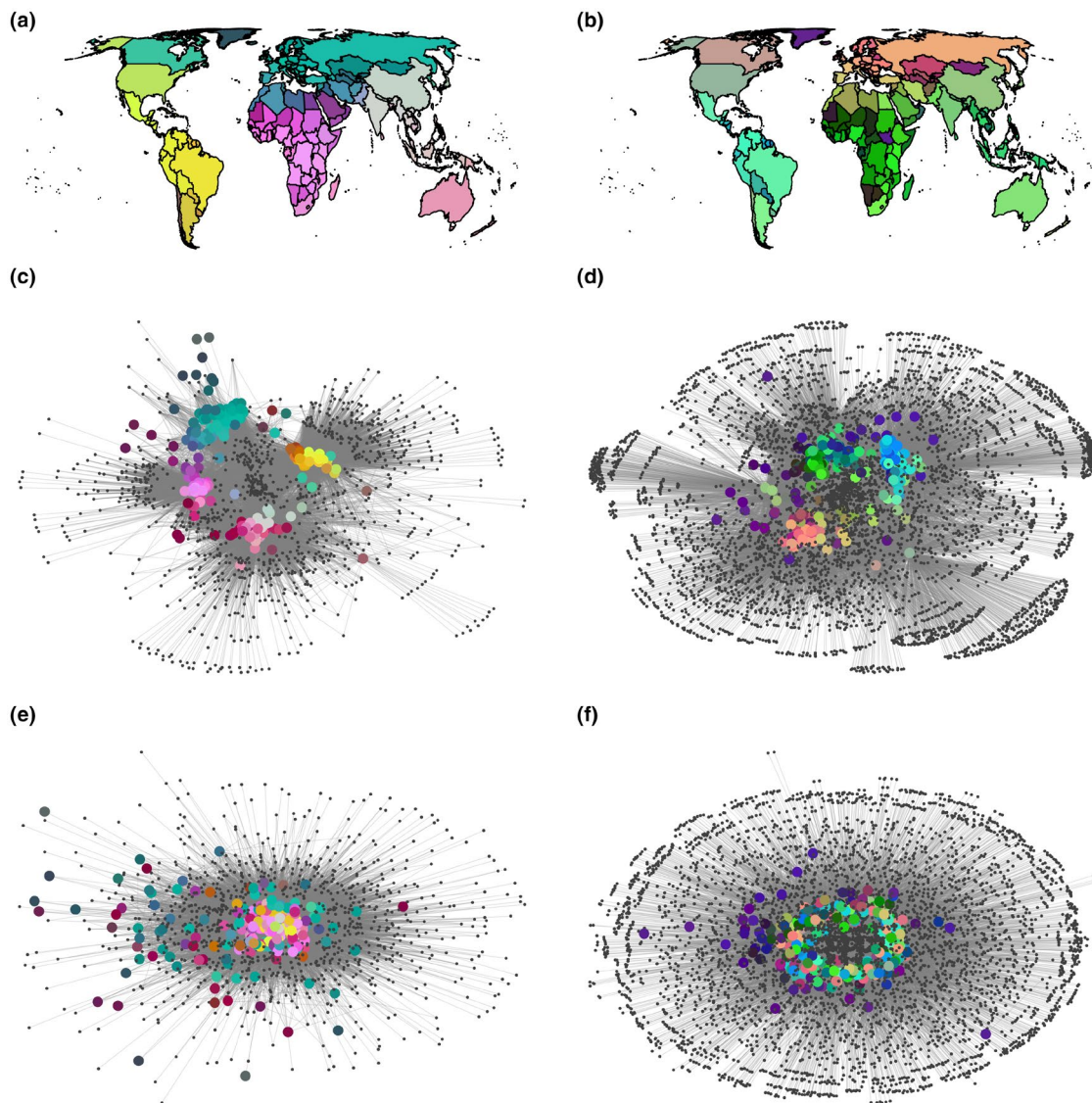


FIGURE 2 Maps of (a) host similarity and (b) pest similarity, (c) observed host-country network (d) observed pest-country network, (e) randomized host-country network, and (f) randomized pest-country network. Colored circles in the networks are countries (matching those in the maps), black points are (b) trees and (d) pests. Countries were colored by conducting multidimensional scaling of pairwise host phylogenetic dissimilarity (UniFrac index, a & c) and pest dissimilarity (Jaccard index, b & d) between countries, and assigning the first three axes to the red-green-blue color model. Similar colors indicate similarity in tree and pest assemblages. Randomized networks (e & f) show expectations if hosts and pests were randomly distributed within countries while maintaining richness within countries, and connectance within the network (proportion of realized links between trees/pests and countries, pest-country connectance: 0.05, host-country: 0.11). Non-random distribution of colors (country nodes) in c & d indicate geographic structure of hosts and pests, compared to e & f. Maps are plotted with an equal-area Eckert IV projection

chromists. Differences in pest composition between countries primarily reflect differences in species identities (turnover) rather than changes in richness (nestedness) (Figure S5), whether assessed across pairs of countries or all countries (proportion of beta-diversity due to pest turnover >98%).

The strong association between host phylogenetic compositions and pest compositions could not be simply explained by a coincidental similarity in bioregionalisation of pests and trees. The empirical correlation between host beta-diversity and pest beta-diversity (Mantel $r = 0.70$) was substantially higher than any selection of

trees (random or exclusively non-hosts) and whether phylogeny was accounted for or not (Mantel r range = 0.46–0.60; Figure S6).

Host breadth, geographic ranges, and saturation

Pest geographical extents were positively associated with pests' host breadth, whether quantified as host phylogenetic diversity ($r = 0.47$, $p < 0.01$), phylogenetic species richness ($r = 0.40$, $p < 0.01$), or phylogenetic species variability ($r = 0.15$, $p < 0.01$) (Figure 5, Figures S7, S8). This

positive association was consistent across pest types, with the exception of nematodes, which tended to have a negative association between geographic extent and phylogenetic species variability. While phylogenetic host breadth predicts pest geographic extent, pests tend not

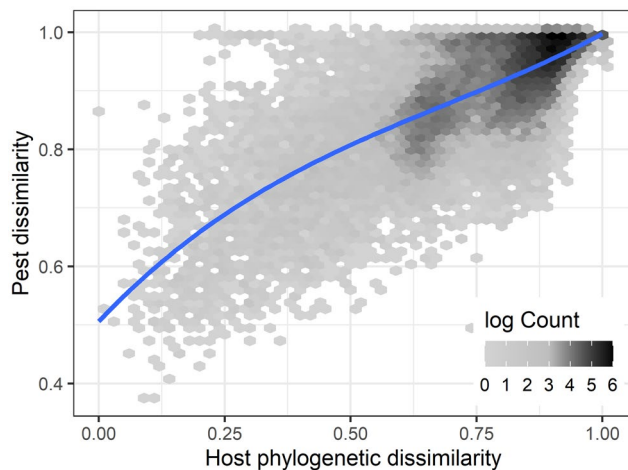


FIGURE 3 Relationship between host (genera) phylogenetic dissimilarity (UniFrac) and pest assemblage dissimilarity (Jaccard index) between countries. The blue line is a third order polynomial regression to illustrate the directionality of the trend, and is not used to assess significance (Mantel $r = 0.70$). The shading gradient indicates the natural log number of points that fall within each cell. See Figure S4 for an equivalent figure with species-level hosts

to fill the geographic ranges of their hosts. On average, pests were recorded in a median of 5.7% of countries where host genera are native, and 20.8% of countries where host species are native (Figure 6). Range filling varied among arthropods (median host genus saturation: 5.3%, median host species saturation: 21.4%), fungi (genus: 5.8%, species: 20.0%), bacteria (genus: 8.0%, species: 25.0%), nematodes (genus: 9.8%, species: 23.3%), viruses (genus: 10.5%, species: 24.1%) and chromists (genus: 14.3%, species: 24.5%). A considerable number of pests occur only in countries where host trees were non-native (genus: 14.4%, species: 23.2%), likely due to many tree species being planted outside their native ranges, and undersampling of pests in their native range, where they may not be considered pests.

DISCUSSION

Despite vast differences in biology, body size, dispersal mechanism, and growth form among arthropod, bacterial, fungal, and nematode tree pests, each responded strongly to the phylogenetic composition of their tree hosts, and more weakly to climate and geographic distances. The link between host phylogeny and pest biogeography is similarly evident in the positive association between host phylogenetic diversity and pest geographic extent—together revealing the primary role

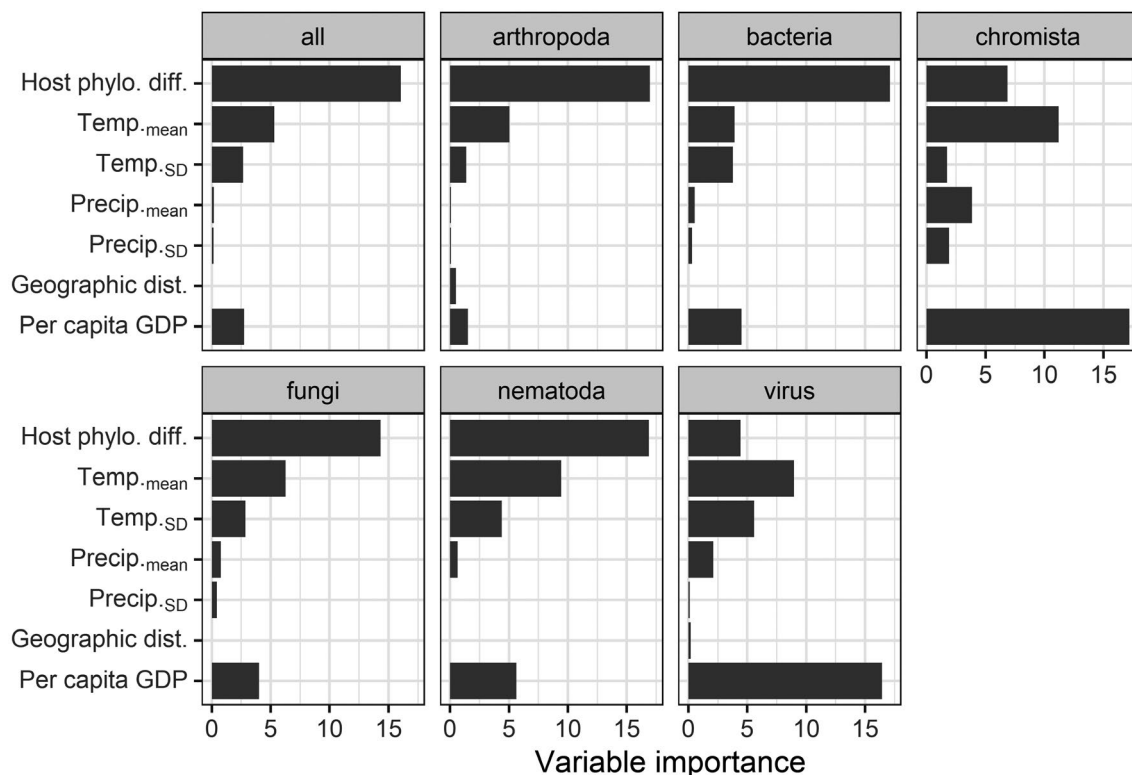


FIGURE 4 Importance of predictors used in generalized dissimilarity models, fit for all pests in aggregate ('all'), and separately for arthropods, bacteria, chromists, fungi, nematodes, and viruses. Importance is calculated as the mean percent decrease in deviance explained when variables are permuted. Temp = temperature; Precip = precipitation

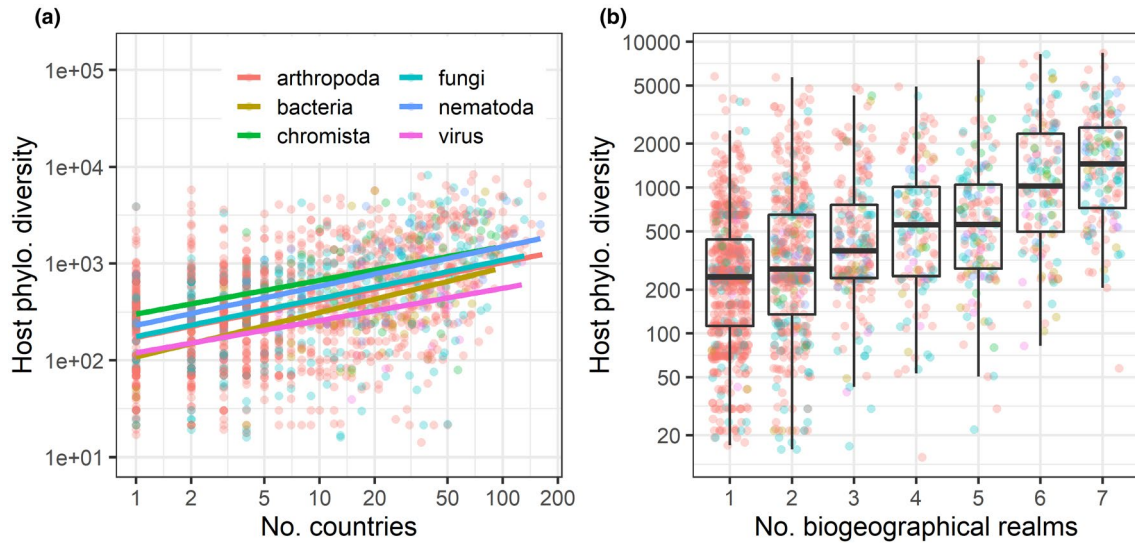


FIGURE 5 Relationship between pests host breadth (genus phylogenetic diversity) and geographic extent, measured as (a) number of countries and (b) number of biogeographical realms where pests have been documented with native hosts. Pests that only exist in countries or realms outside the native range of its hosts were removed. The solid lines in (a) are least squares regressions for each pest type. Note each axis, except the x-axis in (b), has been natural log transformed. See Figure S7 for an equivalent figure with species-level hosts

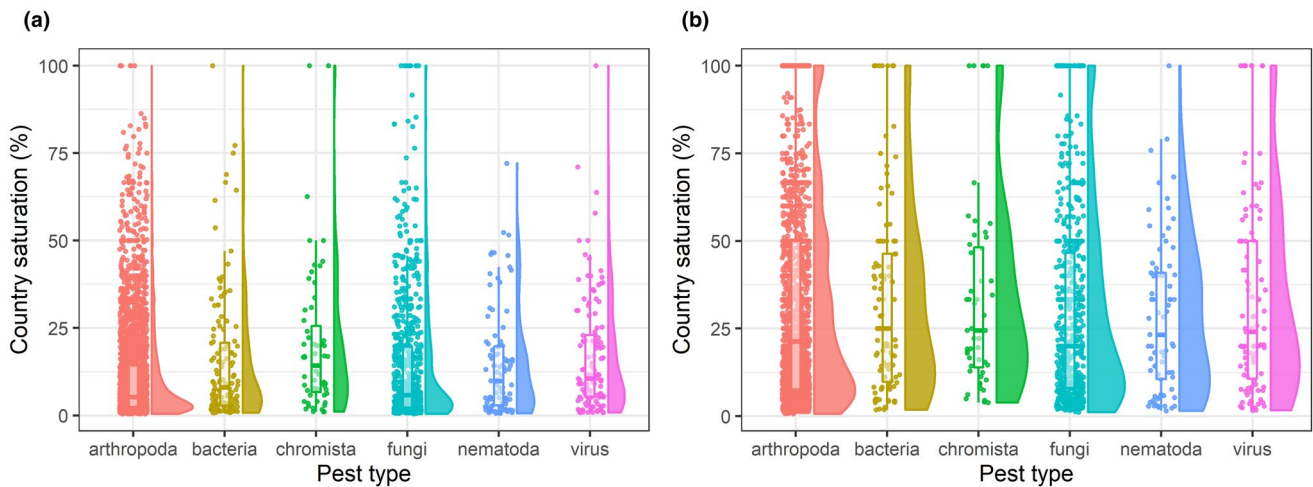


FIGURE 6 Country saturation of arthropods, bacteria, chromists, fungi, nematodes, and viruses with (a) genus-level hosts and (b) species-level hosts. Country saturation is calculated as the number of countries where pests occur with native hosts, divided by the number of countries with native hosts. Greater saturation indicates that pests occupy a larger proportion of their host native geographic extents. Protists, molluscs, and pests of unknown etiology are not shown

of host phylogeny in controlling the global distribution and composition of tree pests. Few pests, however, fill the entirety of their host's geographic extents, indicating factors other than host availability play a role in limiting the distributions of individual pest species. These findings suggest that the distributions of many pests could significantly expand in the future if the geographic, climatic, or ecological barriers limiting their current extents are lowered, and/or that the realised range of some pests may be greater than that currently documented.

Global drivers of pest compositions and extent

Globally, the geographic structure of tree pest compositions closely matches that of host trees. This association is not easily explained by a spurious similarity in the bioregionalisation of pests and trees, which could occur as a consequence of shared biogeographic history even among non-interacting taxa. Rather, this relationship likely reflects the macroevolutionary link between hosts and pests, specifically the specialisation of many pests on one or a few closely related hosts, the tendency

of closely related hosts to share pests (Figure 1), and the phylogenetic turnover of hosts across regions (Figure 2). Together, these three processes result in a strong association between regional pest compositional differences and host phylogenetic differences that is maintained at regional to global scales.

The weaker contributions of geography and climate, compared to host composition, suggest these factors may have only indirect effects on pest distributions, mainly by affecting the composition of host communities. Perhaps most striking, climate tended to have consistently weaker effects on pest compositions compared to host phylogenetic composition, despite having demonstrable effects on the occurrence and abundance of individual pests at regional and local scales (Hepting, 1963). The weaker effects of climate we report may, to some extent, reflect the geographic scale of our analyses (i.e., countries), which might not capture the spatial scale at which weather/climate directly impacts host-pest interactions (Seem, 2004). Regardless, recent work has shown that the fundamental thermal niches of plant pathogens are constrained by biotic interactions (Chaloner et al., 2020)—suggesting pathogens may not fill their thermal (or other abiotic) niches. The lack of strong, consistent, climatic controls on pest distributions could indicate that many pests are adapted to environmental conditions outside those occupied by their hosts, which has important implications for understanding pests ability to track their hosts in future climates and outside their native ranges.

The importance of host phylogenetic affinity is further evidenced by the close relationship between a pest's geographic extent and the phylogenetic breadth of its hosts. We suggest that the evolutionary hurdles to utilising phylogenetically distant host species might present a more significant constraint to pest ranges than geographic distances. This signal may already be present in our data, as host compositions responded more strongly to geographic distance than pest compositions—consistent with a greater homogenisation of pest communities. The reduced importance of geography on pest compositions may reflect the increased flow of goods ground the globe in recent decades which has acted to effectively shortened geographic distances (Helmus et al., 2014), while no analogous mechanism has acted to 'shorten' phylogenetic distances to allow pests to overcome the defences of distantly related hosts. As such, the imprint of geographic distance, and potentially climate, on pest compositions has likely diminished over time with globalisation, while the ability of pests to overcome host defences has been unchanged.

Of the six pest types assessed individually, only chromists and viruses differed meaningfully from other pest types in showing a relatively strong effect of country per capita GDP relative to phylogenetic host composition. The importance of GDP potentially indicates an important sampling effect on the composition of chromists

and viruses. As both viruses and chromists are microorganisms that often cause nonspecific visual signs/symptoms and require laboratory tests to accurately identify (e.g., Jeong et al., 2014; O'Brien et al., 2009), it is perhaps not surprising if detection rates tend to be greater in wealthier countries. Our results indicate that greater sampling and testing is likely required in both wealthy and less wealthy countries to understand the full ecological and biogeographical controls on chromist and virus compositions.

Host range filling

Although most pests fill only a small portion of their hosts geographic range, our results provide some support that microorganisms occupy a larger proportion of their hosts native ranges than macroorganisms, although differences were not large and varied somewhat whether host genera or species were considered. In general, species-level saturation was higher than genus-level saturation as host species tend to have narrower ranges than genera. The lack of range filling, and its variability by pest type, in general, could be indicative of important factors, other than host availability, limiting pest distribution (such as dispersal mechanism, the occurrence of natural enemies, or complex multi-host lifecycles), it is also possible that it could be indicative of undersampling of pest occurrences. The metrics of beta-diversity used in this study are relatively robust to geographic under sampling (Schroeder & Jenkins, 2018), and compositional differences were largely attributable to species turnover rather than nestedness. Nonetheless, our metric of range filling does not readily distinguish between true absences and unreported/undetected occurrences, and the geographic pattern of pest richness in our dataset suggests some countries may have a substantial number of undocumented pest diversity (Figure S9). Absolute values of range filling, hence, should be interpreted with caution, and new occurrences could result from either pests expanding their ranges or through improved detection and reporting.

While pest richness varies substantially between countries (Figure S9), when pest occurrences are standardised by the regional occurrence of their hosts, a more equitable picture emerges. Five of seven biogeographic realms assessed had a similar proportion of potential pests recorded in countries (32%–47% saturation)—the exceptions being Eurasia (saturation: 68%) and Oceanic Islands (saturation: 20%) (Figure S10). High saturation in Eurasia is likely due, in part, to the unique biogeography of the region (i.e., a large, continuous landmass with an east-west orientation and a high number of shared tree taxa), but also the presence of well-developed systems to identify and document tree pests. In contrast, low saturation in Oceanic Islands likely reflects both the unique biogeography of this realm (i.e., small, distantly spaced

land masses, with unique tree compositions) and perhaps reduced documentation in the Western literature (as has been found for some larger countries; Bebbler et al., 2019). Our results suggesting substantial undocumented pest diversity imply that targeted, systematic pest sampling would reveal a considerable number of new pest occurrences (such as those documented by Graziosi et al., 2020).

Predicting future pests and undocumented pest diversity

Our analysis of pest geographic saturation has implications for identifying pests that could become invasive in the future. Our results suggest that pests with large, phylogenetically diverse host breadths, but currently restricted geographic extents, potentially have the greatest opportunity to expand their ranges if introduced outside their current range. In an extreme example, the white-marked tussock moth, *Orgyia leucostigma*, utilises over 70 tree host genera which are widely distributed in the Holarctic, but is currently endemic to North America (known host genera occur in 230 countries of 233 assessed). Other pests that have recently been introduced outside their native range have similarly low saturation (e.g., *Lycorma delicatula* [spotted lanternfly], saturation: 3.9%; *Phytophthora kernoviae*, saturation: 2.1%), suggesting saturation could be a useful metric for identifying pests that may warrant surveillance and greater research. The ten pests with the lowest global saturation in our dataset are shown in Table S1.

Regions vulnerable to future invasion can also be identified by examining the geographic pattern of current host-pest associations. Pests that only occur on hosts outside their native ranges have the potential to be damaging to natural populations if introduced into the host's native range (e.g., Branco et al., 2015). For instance, white pine blister rust (caused by *Cronartium ribicola*, native to Asia), was introduced to North America when infected white pine (*Pinus strobus*) seedlings—native to North America—were (re)imported from Europe in the early 1900s (Kinloch, 2003), and exposed at least eight susceptible North American pines to the pathogen (Liebhold et al., 2013). Emerald ash borer, another non-native tree pest in North America, was similarly known to damage planted *Fraxinus americana* trees in China decades before the pest was introduced into North America (Wang et al., 2010). Approximately 14% of the pests we assessed were documented only outside the native range of tree host taxa, suggesting importation of native plant material grown abroad could be an important, but under-appreciated, pathway for non-native pests to be introduced to host native ranges (Liebhold et al., 2012; Meurisse et al., 2019), that may warrant increased surveillance.

Summary

Tree pests, which include a wide variety of free-living and endoparasitic organisms across multiple taxonomic Kingdoms, showed strong responses to geographic patterns of host phylogenetic compositions. The association between pests and host phylogeny at macroscales confirms that biological interactions largely control the global composition of tree pests, and underscores the importance of host phylogeny to understanding pest impacts on hosts (Gilbert et al., 2015; Mech et al., 2019). While changing climate will undoubtedly reshape the distribution of some pests, it is possible that the greatest immediate impacts of climate change will be on the severity of pest outbreaks (Haynes et al., 2014; Jactel et al., 2019). Understanding pests host ranges and pest physiological responses to climate is thus crucial to forecasting future pest invasions and the threats pests pose to tree biodiversity.

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AUTHORSHIP

AVG & TJD conceived the study. AVG conducted the analyses and led the writing with substantial contributions from TJD.

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SUPPORTING INFORMATION

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