

Responses of plant–pathogen interactions to precipitation: Implications for tropical tree richness in a changing world

Valerie R. Milici  | Dipanjana Dalui | James G. Mickley  | Robert Bagchi 

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

Correspondence

Valerie R. Milici

Email: valerie.milici@uconn.edu

Funding information

American Philosophical Society Lewis and Clark Fellowship; Tinker Foundation; El Instituto Pre-Doctoral Fellowship; The University of Connecticut EEB Botany Award; NSF, Grant/Award Number: DEB-1557086

Handling Editor: Jason Fridley

Abstract

1. Tropical tree-species richness is positively correlated with annual precipitation, but the mechanisms remain unclear. Phytopathogens promote tree-species coexistence by disproportionately afflicting seedlings of locally abundant species, generating a rare species advantage. We consider whether increased plant–pathogen interactions in humid conditions favourable for phytopathogens could drive the precipitation–richness relationship by accentuating the rare species advantage.
2. Support for this mechanism requires that increases in disease under humid conditions disproportionately affect locally abundant species without spreading to rarer species. This criterion would be augmented by either increased phytopathogen host-specificity under humid conditions, or increased asynchronicity in germination of different tree species.
3. Research suggests that precipitation increases the rare species advantage. Increased precipitation enhances phytopathogen transmission, making escape from specialist pathogens more difficult. Additionally, drought stress predisposes plants to disease, especially by opportunistic pathogens. As seasonality in wet forests decreases, scope for asynchronous germination among species increases, potentially concentrating disease transmission within species.
4. *Synthesis.* The pathways we identify could drive the precipitation–richness relationship, but finding direct evidence for them remains a priority. Researching these pathways is especially important because decreasing precipitation due to climate change could disrupt key species coexistence mechanisms and erode tree-species richness.

KEYWORDS

coexistence mechanism, diversity gradient, Janzen–Connell hypothesis, plant–pathogen interactions, precipitation gradient, species richness, storage effect, tropical tree diversity

1 | INTRODUCTION

The remarkable species richness of tropical forest tree communities has fascinated ecologists for centuries (Gillett, 1962; von Humboldt & Bonpland, 1814; Wallace, 1855). Over a thousand tree species can co-occur in half a square kilometre of tropical rainforest (Anderson-Teixeira et al., 2015; Valencia et al., 2004) raising the question of

how species richness can so markedly exceed the number of limiting resources. Numerous mechanisms for tree-species coexistence in tropical forests have been proposed to answer this question and evaluating these mechanisms presents an important task to ecologists (Leigh et al., 2004; Wright, 2002).

A unifying principle in modern coexistence theory is provided by the invasibility criterion, whereby the species in a community can stably

coexist if each species can increase from rarity when the other species in the community are at their equilibrium abundances (Chesson, 2000). When the invasibility criterion is met, rare species in the community will gain an advantage, thereby preventing competitive exclusion. It has long been recognized that pathogens can play a role in stabilizing coexistence of their host species (Bever, Westover, & Antonovics, 1997; Gillett, 1962; Holt & Pickering, 1985). Rare host species gain an advantage over their more common competitors provided that pathogen transmission is greater within than among host species (Dobson, 2004; Holt & Pickering, 1985). Barriers to pathogen transmission among host species prevent disease on abundant host species from spreading to co-occurring rare host species, which can grow unchecked until they are abundant enough to support large populations of their own pathogens.

Two mechanisms frequently invoked to explain the high local tree-species richness (alpha diversity) of tropical forests could be driven by phytopathogens, particularly fungi and oomycetes. The Janzen–Connell effect (Connell, 1971; Janzen, 1970) predicts that host-specific natural enemies generate a rare species advantage by disproportionately reducing recruitment in seedlings occurring at high conspecific densities or near their parents (conspecific negative density dependence, CNDD). The Janzen–Connell effect has received extensive support both theoretically (Armstrong, 1989; Levi et al., 2019; Sedio & Ostling, 2013) and empirically (Augspurger, 1984; Bagchi et al., 2014; Comita et al., 2014; Mangan et al., 2010; Packer & Clay, 2000). Fungal and oomycete phytopathogens appear to be important natural enemies for mediating the Janzen–Connell effect (Augspurger, 1984; Bagchi et al., 2014; Krishnadas, Bagchi, Sridhara, & Comita, 2018; Mangan et al., 2010). Under the Janzen–Connell effect, transmission of pathogens among tree species is restricted by the host-specificity of phytopathogens, leading to a rare species advantage. A second coexistence mechanism, the storage effect (Chesson & Warner, 1981), is gaining attention in the tropical forest literature (Kelly & Bowler, 2002; Usinowicz et al., 2017; Usinowicz, Wright, & Ives, 2012). Although the storage effect is often framed in terms of resource competition (Adler, HilleRisLambers, Kyriakidis, Guan, & Levine, 2006; Angert, Huxman, Chesson, & Venable, 2009), shared generalist phytopathogens could mediate storage effects via apparent competition (Mordecai, 2015). Under storage effects, temporal separation of seedling vulnerability to phytopathogens creates the barrier to transmission among species that generates a rare species advantage. Put simply, the Janzen–Connell hypothesis limits transmission among species through phytopathogen host-specificity while pathogen-mediated storage effects limit pathogen transmission through temporal variation in tree seedling availability to phytopathogens.

The ability to explain relationships between species richness and local environmental gradients provides a powerful test for coexistence mechanisms. Within the tropics, precipitation (and related measures of moisture, such as seasonality) is the best environmental predictor of tree-species richness, with species richness generally higher in wet tropical forests (Francis & Currie, 2003; Gentry, 1988; Hawkins et al., 2003; Kref & Jetz, 2007). Several mechanisms could contribute to this pattern, including filtering of drought-intolerant species from dry forests (Engelbrecht et al., 2007), greater

energy availability in less stressful environments allowing larger communities and hence more species (Wright, 1983) and narrow niche breadth in less variable environments (Janzen, 1967). In addition, it has long been suggested that interactions between trees and their natural enemies are strengthened under increasing precipitation (Connell, 1971; Gillett, 1962; Givnish, 1999), possibly enhancing the ability of natural enemies to maintain tree-species coexistence. However, empirical tests of this hypothesis are lacking. In plants, disease is the outcome of the interaction between a plant host, its pathogen and the environmental context, a relationship referred to as the disease triangle (Agrios, 1997; Liu & He, 2019). Shifts in precipitation can alter both plant and phytopathogen physiology, which may change the outcome of their interaction. It is possible that both Janzen–Connell and storage effects intensify under wetter and more aseasonal conditions, contributing to the greater species richness of wet forests (Gillett, 1962; Givnish, 1999). Projections that large areas of the tropics will become drier due to climate change (IPCC, 2014; Lintner et al., 2012; Malhi et al., 2008) add impetus to examinations of the links between precipitation and species richness. Identifying the mechanisms that generate the precipitation–richness relationship may allow us to anticipate previously unappreciated consequences of climate change for biodiversity.

Here we consider three pathways (roman numerals in Figure 1) through which the positive relationship between precipitation and tree diversity can be caused by the effects of precipitation on

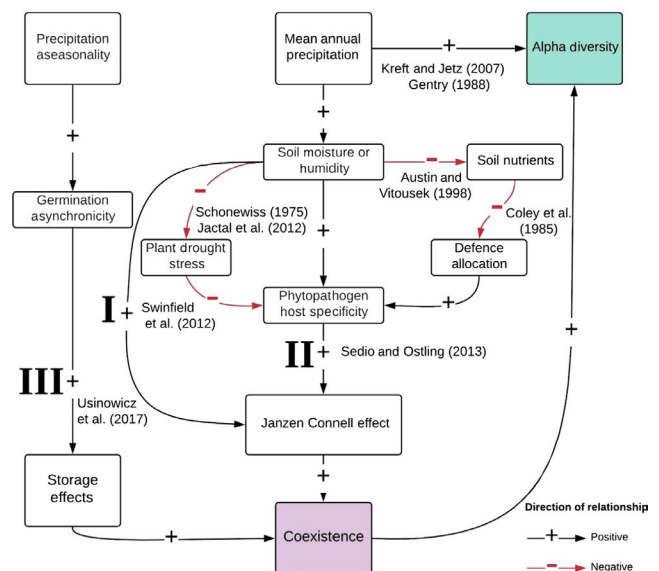


FIGURE 1 Schematic diagram of the proposed pathways through which phytopathogens could lead to the precipitation–tree diversity relationship. The bold roman numerals indicate the three main pathways proposed in this paper, each consisting of multiple links. Arrows with plus (minus) symbols indicate positive (negative) relationships between the boxes they connect. The effects of paths in series are multiplicative, so boxes connected by a sequence of two negative paths are positively related to each other. Support for particular pathways from the literature is indicated by the references next to the arrows [Colour figure can be viewed at wileyonlinelibrary.com]

plant–phytopathogen interactions. These scenarios are (I) stronger control of host populations through CNDD by existing host-specific phytopathogens, (II) increased specificity of interactions and (III) increased storage effects.

2 | THE EFFECTS OF MOISTURE ON THE STRENGTH OF CNDD

First, increased moisture could strengthen existing CNDD (Figure 1, Pathway I) by making it more difficult for a seedling to escape its specialist phytopathogens. Here we consider impacts of moisture availability on phytopathogens that are at least moderately host-specific; increasing impacts of generalist phytopathogens could erode species richness as the best defended plant species exclude the rest through apparent competition (Chesson & Kuang, 2008). This assumption is consistent with the literature, which suggests many phytopathogens are competent on multiple host species, with their infection probabilities and negative effects on hosts declining as phylogenetic distance between hosts increases (Gilbert, Briggs, & Magarey, 2015; Gilbert & Webb, 2007). Moisture availability has a positive effect on the ability of both above- and below-ground phytopathogens to disperse to and infect hosts (Garrett, 1970; Rossi & Caffi, 2011; Short & Lacy, 1974; Swinfield, Lewis, Bagchi, & Freckleton, 2012). Above-ground, almost all foliar pathogens are better able to cause disease as moisture increases (Colhoun, 1973). Furthermore, splash dispersal is an important component of spore dispersal for many foliar pathogens, so increased frequency of precipitation can promote disease (Colhoun, 1973; Swinfield et al., 2012; Yarwood, 1978). For below-ground pathogens, soil moisture impacts the ability of a spore to germinate and infect a susceptible host (Garrett, 1970; Short & Lacy, 1974). As moisture increases, so does the amount and diffusion of root exudates in the soil. These exudates both signal the presence of a susceptible host to the pathogen, and serve as a nutrient source that increases pathogenicity (Garrett, 1970; Kerr, 1964; Short & Lacy, 1974). As a result, spores germinate sooner and at greater distances from the host under wetter conditions (Short & Lacy, 1974), infecting a higher percentage of hosts (Kerr, 1964). Moisture, therefore, can facilitate the movement of both above- and below-ground phytopathogens. Increasing the distance a pathogen can transmit to a new host increases the distances conspecific seedlings must maintain among themselves and from conspecific adults to find enemy-free space and escape pathogen attack (Figure 2a). Such increases in the distance necessary to escape phytopathogens from conspecifics strengthen the potential for tree-species coexistence (Levi et al., 2019; Murrell & Law, 2003) by accentuating the rare species advantage, and enable a higher number of species to coexist in wetter forests.

Precipitation seasonality could also affect plant–phytopathogen interactions through its influence on fungal and oomycete spore survival. In seasonal environments, pathogens produce long-lived spores, which survive the dry season to initiate infections at the onset of the following wet season (Agrios, 1997). This initial pulse of infection may be important for forest dynamics because it coincides with seedling

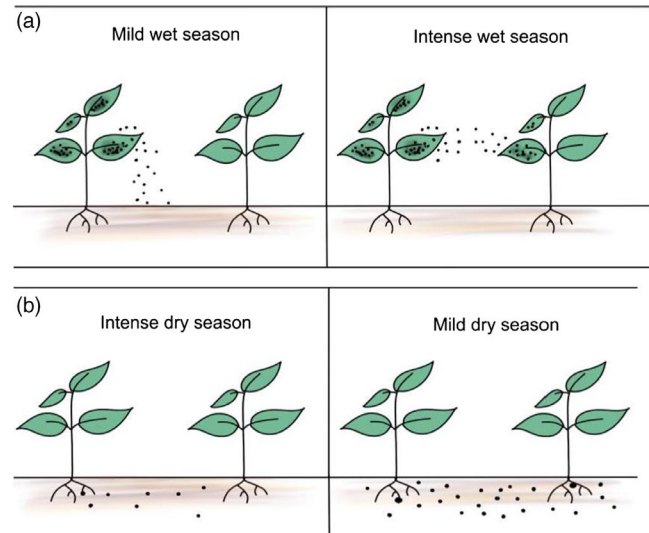


FIGURE 2 Increased precipitation and aseasonality can promote the ability of phytopathogens to cause disease in their hosts. Increased disease can translate to greater potential for tree-species coexistence and richness if the phytopathogens are at least partially host-specific. (a) As the intensity of the wet season increases, a pathogen can transmit to more distant hosts because more frequent precipitation events increase splash dispersal above-ground, making it more difficult for a seedling to escape its enemy, and increasing conspecific negative density dependence (CNDD). (b) A greater proportion of phytopathogen spores can survive milder dry seasons, increasing the density of viable spores density in the soil at the start of the following wet season. The higher viable spore density hastens the onset of infection in the seedling community where the dry season is mild. Young seedlings are more susceptible to pathogen attack, therefore communities that suffer earlier infection will experience greater mortality and CNDD [Colour figure can be viewed at wileyonlinelibrary.com]

germination, the stage when seedlings are at their most vulnerable (Develey-Rivière & Galiana, 2007; Garrett, 1970). Spores lose viability at both very high and very low moisture (Griffin, 1978; Hong, Ellis, & Moore, 1997; Williams, Shameemullah, Watson, & Mayfield, 1972). Therefore, viable spore density at the onset of the wet season is likely to peak where dry seasons are short and of intermediate intensity (Figure 2b). Low spore density delays an epidemic (Van der Plank, 1963), and seedlings germinating after intense dry seasons may have more time before infection risk than seedlings where the dry season is weak. This delay in infection risk provides an opportunity for seedlings to develop their defences, or physically outgrow infection risk (Develey-Rivière & Galiana, 2007; Garrett, 1970). This increased resistance to disease would increase seedling survival and reduce CNDD, decreasing the ability of phytopathogens to control tree populations in dry and seasonal forests. Thus, the effect of seasonality on spore density could lead to increases in CNDD as aseasonality increases.

In summary, by creating favourable conditions for phytopathogen spore survival and dispersal, wet and aseasonal climates can reduce the ability of tree seedlings to find disease-free space. As a result, the rare species advantage will strengthen if phytopathogens are at least partially host-specific. Although a number of studies have

investigated these relationships in agricultural contexts (Garrett, 1970; Short & Lacy, 1974; Yarwood, 1978), data from species-rich natural communities are scant, especially any collected along precipitation gradients. Such data will be necessary to determine if wetter conditions extend the distance over which phytopathogen transmission can occur and if aseasonal conditions increase spore longevity. Experiments that relate precipitation to the distance from conspecifics from which phytopathogens are able to inhibit recruitment would be particularly useful to test the mechanisms proposed above. An additional line of enquiry could examine patterns of phylogenetic clustering of host communities. Because closely related plant species tend to share phytopathogens (Gilbert et al., 2015; Gilbert & Webb, 2007), phylogenetic clustering of tree assemblages at small spatial scales should decline when they are strongly structured by disease (Webb, Gilbert, & Donoghue, 2006). We might therefore expect that in wet environments phytopathogens will reduce the phylogenetic clustering of trees communities through ontogeny more markedly than in dry environments.

3 | THE EFFECTS OF MOISTURE ON HOST-SPECIFICITY

In addition to strengthening the existing CNDD, a second way that the Janzen–Connell effect may increase along a moisture gradient is through increased host-specificity of fungal and oomycete phytopathogens (Figure 1, Pathway II). A key assumption of the Janzen–Connell hypothesis is that plant populations are regulated by specialist natural enemies such as host-specific pathogens (Connell, 1971; Janzen, 1970). However, phytopathogens are often not strict specialists, and can infect related species in a pattern that decays with phylogenetic dissimilarity of the host species (Gilbert & Webb, 2007). Pathogen sharing does not preclude phytopathogens from facilitating tree-species coexistence, but the capacity for coexistence increases with increasing host-specialization of phytopathogens (Sedio & Ostling, 2013). If moisture availability positively impacts host-specialization in phytopathogens, competition among seedlings will become further concentrated within species and promote species coexistence. We outline two ways in which moisture availability may impact host-specialization in fungal and oomycete phytopathogens (Figure 1): (a) through plastic responses of seedlings and phytopathogens to geographical and temporal variation in moisture availability, and (b) through an evolved response to a longstanding gradient in wet/dry seasonality.

3.1 | Temporal and geographic variation in moisture availability

Moisture may impact the host-specificity of phytopathogens due to the seedling's physiological response to water availability. This could occur along moisture gradients within the geographic range of a host's distribution, or due to interannual variation in water availability (e.g. driven by El Niño Southern Oscillation, ENSO). Drought stress

may predispose plants to disease by weakening their defence metabolism, enabling phytopathogens to overcome defences that previously suppressed them and cause disease in the host (Schoeneweiss, 1975; Figure 3a). Phytopathogens often infect both susceptible and resistant hosts, but can only overcome the defences of susceptible hosts to cause disease symptoms (Schoeneweiss, 1975). As a result, susceptibility induced by drought stress likely increases disease more from generalist than specialist phytopathogens. The interaction between

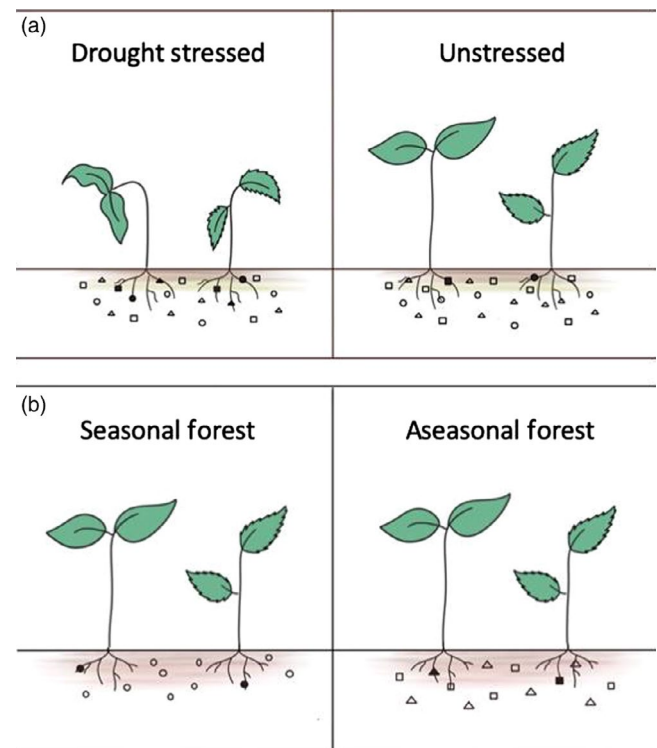


FIGURE 3 Drought can reduce the specificity of plant-phytopathogen interactions through two mechanisms. Here conspecifics are denoted by identical seedling morphology, while heterospecifics are denoted by different morphologies. (a) Tree seedlings experiencing water stress due to drought, or because they are at the edge of their geographic range, will become susceptible to a wider range of pathogens (denoted by shapes on roots; successful infections are filled shapes) than under non-stressed conditions. This decrease in pathogen specificity due to weakened plant immune systems will reduce conspecific negative density dependence (CNDD) under dry/drought conditions because generalist pathogen infections will occur across tree species, regardless of conspecific tree density. (b) Lack of pathogen pressure during the dry season in dry/seasonal environments, or abundant soil nutrients favouring fast growth-low defensive allocation strategies, weakens selection on trees for strong defences against pathogens, in turn lowering selection for pathogens to evolve host specificity to combat those defences, leading to more generalist pathogens. The more continuous pathogen pressure experienced in wet/aseasonal forests, and limiting soil nutrients, strengthens selection on trees to evolve defences against pathogens and on pathogens to evolve host-specific mechanisms to overcome those defences, leading to more specialist pathogens. With increasing host-specificity, pathogens generate increased CNDD [Colour figure can be viewed at wileyonlinelibrary.com]

drought stress and plant disease is well-documented in the literature (Coolen et al., 2016; Desprez-Loustau, Marçais, Nageleisen, Piou, & Vannini, 2006; Jactel et al., 2012; McElrone, Sherald, & Forseth, 2003; Sinha, Irulappan, Mohan-Raju, Suganthi, & Senthil-Kumar, 2019; van Niekerk, Strever, Toit, Halleen, & Fourie, 2011). The two stressors are additive (McElrone et al., 2003), with plants exposed to both water and disease stress generally experiencing the greatest symptom development (Coolen et al., 2016; Sinha et al., 2019; van Niekerk et al., 2011). A plant's response to stress is dominated by the most recent stress (Coolen et al., 2016), so a plant that is resistant against initial pathogen exposure may become susceptible to a generalist pathogen after the onset of water stress (Coolen et al., 2016; Ramegowda & Senthil-Kumar, 2015), consistent with the predictions of predisposition (Schoeneweiss, 1975). Although the majority of the research on water stress and phytopathogens has been performed in the context of agriculture, drought does appear to increase disease incidence in natural tree communities as well (Desprez-Loustau et al., 2006), especially in the case of foliar pathogens (Jactel et al., 2012). Therefore, we expect that hosts experiencing drought stress will be susceptible to a wider range of pathogens than hosts of the same species in a wetter environment, weakening CNDD. Concomitantly, this will result in a strengthening of CNDD in a host species as annual precipitation or aseasonality increases along the host's range. We also expect that this generates weaker CNDD during dry years, such as during ENSO events.

3.2 | Seasonality and the evolution of specificity

A regional wet/dry seasonality gradient may create a pest pressure gradient, or a nutrient gradient, that selects for host-specific natural enemies in aseasonal/wetter forests (Connell, 1971; Gillett, 1962; Givnish, 1999; Figure 3b). In seasonally dry forests, dry periods lower pathogen spore viability, weakening their ability to control host populations through the establishment of new infections. As a result, pathogen pressure is not constant in seasonally dry forests, and may weaken selection on trees for high defensive allocation. In aseasonal forests, pathogen pressure is constant throughout the year, strengthening selection for trees to invest in defence against natural enemies (Connell, 1971). As a result, in an aseasonal forest, few generalist natural enemies can successfully attack a host, biasing towards high levels of host-specificity. Simultaneously, soil nutrients generally decrease as precipitation increases due to increased leaching (Austin & Vitousek, 1998). The high soil nutrients in dry/seasonal forests (Austin & Vitousek, 1998) favour species with fast growth and low defensive allocation, because it is less costly for species to outgrow pathogen damage than it is for them to produce defensive compounds when nutrients are not limiting (Coley, Bryant, & Chapin, 1985). Generalist phytopathogens could be favoured in these forests, as there are few defences that they must overcome to successfully colonize a host. Conversely, the low soil nutrients in wet/aseasonal forests (Austin & Vitousek, 1998) favour species with slow growth and high defensive allocation, because any tissue lost to pathogen damage could be lethal to seedlings when nutrients are

limiting (Coley et al., 1985). Specialist pathogens should therefore be favoured in wet/aseasonal forests because there are many, diverse host defences that pathogens must overcome to successfully colonize a host. The greater number of host-specific phytopathogens in wet aseasonal forests compared to seasonally dry forests would enable more species to coexist in aseasonal forests through stronger CNDD. Furthermore, co-evolution of plants and phytopathogens as they respond to each other's adaptations could promote speciation, increasing the richness of the wider species pool (Fischer, 1960).

To our knowledge, there has been only one attempt (Spear, 2017) to assess whether host-specificity varies among fungal communities that span a seasonality gradient. The fungi encountered by Spear (2017) appeared to have low host-specificity, regardless of precipitation or seasonality, but low sample sizes restricted formal tests of how host-specificity might relate to climate. However, additional experiments on the impact of natural enemies on species distributions may provide clues. Comparisons of plant–fungal (Spear, Coley, & Kursar, 2015) and plant–herbivore (Baltzer & Davies, 2012) interactions that span tropical seasonality gradients have sought to understand if natural enemies limit the distribution of seasonally dry-forest species (Baltzer & Davies, 2012; Spear et al., 2015). Both experiments indicated that species from seasonally dry forests are susceptible to attack in both seasonal and aseasonal forests, while species from aseasonal forests are less susceptible to attack in seasonal forests (Baltzer & Davies, 2012; Spear et al., 2015). The above mechanism may explain this pattern. Seasonally dry forest species can be attacked regardless of provenance, because they are not well-defended and their defences can be overcome by natural enemies from both forests, while aseasonal species are better defended and only susceptible to natural enemies that have evolved mechanisms to overcome their defences. Although it is possible that decreased seasonality may lead to the evolution of increased host-specificity of natural enemies (Connell, 1971), this hypothesis needs much more direct testing.

One way to test this hypothesis would be to quantify the relationships between phytopathogen host-specificity, host plant susceptibility and wet/dry seasonality. We expect that trees from aseasonal forests allocate more to defence, have a wider variety of defensive compounds and are therefore susceptible to a narrower range of phytopathogens than those originating from seasonal forests. The host-specificity of phytopathogens should likewise be greatest in aseasonal forests, with the average phylogenetic distance among tree species that share phytopathogens declining with precipitation. Importantly, trees from seasonal forests may still be susceptible to phytopathogens from aseasonal environments, whereas trees from aseasonal forests should be relatively immune to phytopathogens from seasonal forests.

4 | THE EFFECTS OF MOISTURE ON STORAGE EFFECTS

Increasing moisture may strengthen the effect of existing CNDD, or increase phytopathogen host-specificity, as discussed above. Another barrier to transmission across species may arise if seedlings

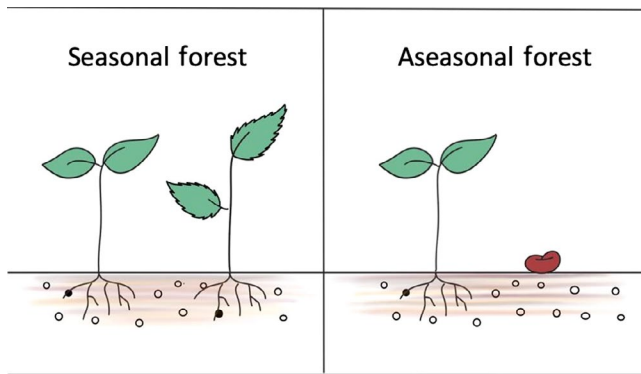


FIGURE 4 Strong seasonality in precipitation synchronizes the phenology of seed germination across tree species so they all germinate while water is not limiting. As a result, generalist phytopathogens on seedlings of one species can spread to those of other species that are vulnerable at the same time. In aseasonal environments, the timing of germination can be staggered among tree species. As a result, diseases can only be transmitted to seedlings of the same host species as other tree species are only present in stages that are less vulnerable to pathogen infection (e.g. seeds or older, better defended seedlings). This separation of when different tree species are vulnerable to infection enables even generalist pathogens to control the abundances of multiple tree species in aseasonal, but not seasonal, conditions. As a result, the advantage to rare species from interactions with phytopathogen will increase as climates become more aseasonal [Colour figure can be viewed at wileyonlinelibrary.com]

of different species emerge at different times, allowing for pathogen-mediated storage effects (Mordecai, 2015; Figure 4). In the case of storage effects, multiple tree species can be controlled by a generalist pathogen.

For a seedling to acquire a pathogen from a diseased neighbour, it must be susceptible to the pathogen at the time of transmission. Given a sufficient interval between germination times between tree species, a disease outbreak in one species may have subsided before the other species germinates, limiting transmission between species. The generalist pathogen will respond to the abundance of each tree species separately, and so high abundances of one species will not lead to increased infection and mortality of the other species.

For storage effects to play a role in species coexistence, communities must meet three conditions (Chesson & Warner, 1981), which tropical forests satisfy. Furthermore, there is some indirect empirical evidence for the storage effect in tropical forests (Kelly & Bowler, 2002; Usinowicz et al., 2012, 2017). First, storage effects promote species coexistence when environmental conditions fluctuate so that each species is the dominant competitor for limited periods of time (Chesson, 2000; Chesson & Warner, 1981). Two recent studies have revealed that the among-species asynchrony in tree fruiting patterns in several tropical forests is consistent with storage effects contributing to species coexistence (Usinowicz et al., 2012, 2017). Usinowicz et al. (2017) found that fruiting of different species peaked at different times of year as well as in different years, especially in tropical forests. Additionally, data from Barro Colorado Island, Panama, suggest that tree species germinate at different times from

each other (Usinowicz et al., 2012), and hence are also most vulnerable to phytopathogens at different times. The second criteria is that species must have a long-lived 'storage' stage that persists while the species is competitively inferior (Chesson, 2000; Chesson & Warner, 1981). Seedlings and adults that survive the early stage of their life are comparatively invulnerable to further pathogen-mediated apparent competition, satisfying the storage condition.

The third and final requirement for storage effects to maintain coexistence is that each species must suffer greater competition in favourable periods than in unfavourable periods (Chesson, 2000; Chesson & Warner, 1981). Such positive covariance between competition and environmental favourability restricts the ability of any species to monopolize resources when conditions make it competitively dominant. Because phytopathogens can respond rapidly to elevated densities of their hosts (Garrett, 1970), they are good candidates for mediating this competition-favourability covariance, even without host-specificity. Therefore, a heterospecific seedling located in a dense aggregation of another species subject to a pathogen outbreak would also be disadvantaged if vulnerable at the same time. For a rare species to gain advantage, it would have to occur at a location or time separated from other species and therefore experience a low density of both conspecific and heterospecific seedlings at the vulnerable stage.

Two aspects of plant-phytopathogen interactions could help satisfy this condition. First, the short duration (a few weeks immediately following germination) that seedlings are particularly vulnerable to pathogens (Develey-Rivière & Galiana, 2007; Garrett, 1970) will reduce the overlap among species in this period of vulnerability. Secondly, seedlings during this early stage may be susceptible to a broader suite of pathogens than later on (Develey-Rivière & Galiana, 2007) and hence different tree species might share a greater proportion of their associated pathogens. Greater overlap in pathogen communities increases the potential for apparent competition among plant species, which could lead to competitive exclusion of more vulnerable species (Holt & Dobson, 2006). However, given that this vulnerable stage is relatively brief (Garrett, 1970), seedlings emerging even a few weeks apart might be unaffected by outbreaks of diseases in the other species.

On the basis of current evidence (Usinowicz et al., 2012, 2017) it appears that storage effects contribute to tree-species coexistence in tropical forests. The scope for storage effects to enable tree-species coexistence may increase with decreasing seasonality (Usinowicz et al., 2017), providing an additional pathway through which increases in annual precipitation may facilitate increased species richness (Figure 1, Pathway III). Within the tropics, drier climates tend to be more seasonal (Gentry, 1988), and climatic seasonality creates abiotic barriers to seedling germination and survival. The abiotic barrier created by the dry season restricts the majority of germination across all tree species to the start of the wet season (Garwood, 1983), providing seedlings with the longest period of favourable conditions before water becomes limited. As dry season duration decreases, the wet season extends, providing greater scope for temporal partitioning of fruiting and germination, thereby enhancing the potential for storage effects. As a result, seedlings of one species have greater opportunity to avoid

contracting a shared generalist pathogen from heterospecific seedlings by germinating at a different time of year. This provides species with time to develop their defences and age out of susceptibility to the generalist pathogen before the germination of another susceptible species. Although each species may be regulated by the same generalist pathogen, temporal partitioning of susceptibility creates a barrier to transmission among species, and concentrates apparent competition within species.

Usinowicz et al. (2017) provided evidence that a latitudinal gradient in seasonality was associated with greater fruiting asynchrony and potential for coexistence towards the equator: a similar analysis along gradients of precipitation seasonality could evaluate the contribution of variation in storage effects to the precipitation–diversity relationship. Experiments that compare seedling performance under factorial combinations of germination synchrony (at the same time or offset from heterospecific species) and phytopathogen access (e.g. using fungicides) could also provide insight into whether phytopathogen-mediated storage effects are important contributors to tree-species coexistence. If storage effects gain in importance with increasing precipitation, germination phenologies should become increasingly segregated with moisture availability and the costs of germinating simultaneously with other species should be greatest in wet forests. Additional evidence for this mechanism would be found if species that temporally segregate germination times in aseasonal forests are more likely to share a generalist fungal or oomycete pathogen than species that germinate at the same time.

5 | CLIMATE CHANGE

The recent past has witnessed a drying trend in many tropical rainforest regions, especially in parts of Africa (Malhi et al., 2008; Malhi & Wright, 2004). General Circulation Models (GCMs) project future precipitation decreases in large portions of Amazonia, Central America and western equatorial Africa (IPCC, 2014; Malhi et al., 2008; Figure 5), while parts of western tropical South America, Central Africa and Southeast Asia could become wetter (Figure 5;

Lintner et al., 2012). A consistent projection of GCMs is that dry areas will get drier and wet areas wetter, thus intensifying precipitation gradients and seasonality (Kirtman et al., 2013; Lintner et al., 2012). Both within- and between-year variation in precipitation may also respond to climate change as monsoons and El Niño–Southern Oscillation (ENSO) are likely to intensify over the 21st century. For example, dry seasons have intensified in northern Amazonia since the 1970s and several GCMs project greater climatic variation and dry season intensification in large parts of the northeastern and southwestern Amazon and Central America (Lintner et al., 2012; Malhi et al., 2008).

The implications of reduced precipitation and drought for tree-species richness are less well resolved. The precipitation–richness relationship hints that altered precipitation could have consequences for species richness, but the time-scales over which any changes might manifest remain unknown. Bunker and Carson (2005) experimentally irrigated naturally recruited seedlings and saplings during a drought in central Panama. Species losses from irrigated plots were significantly lower than observed in the unmanipulated plots unprotected from drought. CNDD was apparent in irrigated plots, but was not noticeable in the unmanipulated, droughted, plots. Thompson, Alvarez-Loayza, Terborgh, and Katul (2010) used simulations from a mathematical model partly parameterized with field data to explore the effects of altered temperature and precipitation on the dynamics of *Irartea deltoidea*, a neotropical palm tree, and its foliar pathogen, *Diplodia mutila*. Increased temperature promoted fungal growth and decreased precipitation reduced palm fecundity, suggesting that the projected climate change for the area would reduce *I. deltoidea* recruitment. However, Thompson et al. (2010) did not consider direct effects of precipitation on the fungal partner, and it is possible that dry conditions could counteract the positive effects of temperature on fungal growth. Overall, these studies raise intriguing hypotheses about the potential for climate change to have indirect consequences for tree diversity by disrupting density dependence in seedlings. However, rigorous tests of these hypotheses require further manipulative experiments. In particular, studies conducted at the level of whole communities that simultaneously manipulate access by groups of natural

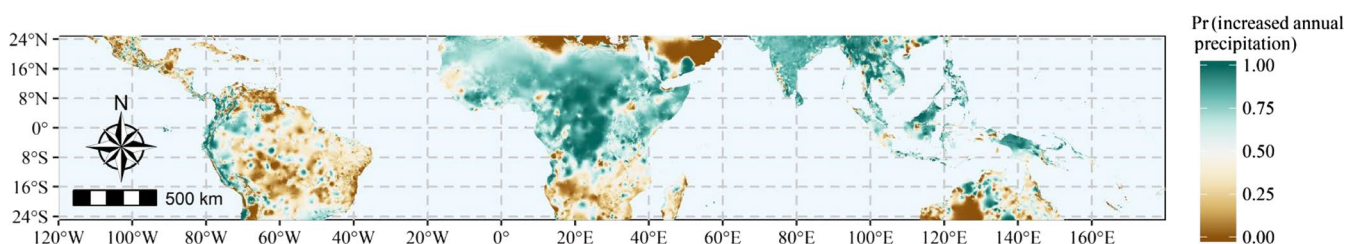


FIGURE 5 Change in precipitation during the 21st century in tropical areas as projected by 17 General Circulation Models (GCM) included in the 5th Coupled Model Intercomparison Project (CMIP5), assuming future greenhouse gas emissions follow Representative Concentration Pathway 8.5 (business as usual). We compared observations of mean annual precipitation for the late 20th century (1970–2000; interpolated to a 2.5° spatial resolution) in each grid cell to that projected by each GCM for the end of the 21st century (2070–2100; downscaled to a 2.5° resolution). The rank of the observed 20th century precipitation compared to the GCM projections roughly translates to the probability with which GCMs project an increase in mean annual precipitation in the grid cell during the 21st century. Data were obtained from WorldClim, versions 1.4 for future climate & 2.0 for late 20th century climate (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) [Colour figure can be viewed at wileyonlinelibrary.com]

enemies (e.g. Bagchi et al., 2014; Krishnadas et al., 2018) and water availability (e.g. Bunker & Carson, 2005; Paine, Harms, & Ramos, 2009) will be necessary to test for a causative link between moisture availability and the contributions of fungal pathogens to tree-species coexistence.

6 | CONCLUSIONS

Strengthening effects of phytopathogens on tree populations in wetter climates could contribute to driving the relationship between precipitation and tree-species richness in the tropics. As we outline here, wetter and aseasonal climates could enhance fungal and oomycete phytopathogen contributions to the Janzen–Connell effect by enhancing existing CNDD or by increasing phytopathogen host-specificity, and phytopathogen-mediated storage effects through asynchronicity of germination times in aseasonal forests. Additionally, the mechanisms outlined in this paper could interact with one another—for example, partially host-specific pathogens could mediate coexistence of tree species with similar germination phenology that do not share pathogens, while tree species that share pathogens may avoid interspecific pathogen transmission by germinating asynchronously. Much of the evidence for the pathways we present in this paper is indirect—few studies have set out to explicitly link the effectiveness of a phytopathogen-mediated tree-species coexistence mechanism to an environmental gradient. We hope these ideas spur future research that examines these links for two reasons. First, examining whether these coexistence mechanisms contribute to variation in tree-species richness along environmental gradients provides a stringent test of their importance. Second, should the precipitation–diversity relationship reflect the outcome of processes that define the species richness of a community, decreased precipitation, as projected for large parts of the tropics under climate change, could reduce tree-species richness of some of the most biodiverse regions of the planet.

ACKNOWLEDGEMENTS

We would like to thank Owen Lewis, Rachel Gallery, Sofia Gripenberg, Annette Ostling, Joe Wright, Liza Comita, Greg Gilbert and Jonathan Klassen for their contributions to these ideas over many years. This research was supported by funding to V.R.M. (Tinker Foundation, El Instituto Pre-Doctoral Fellowship, The University of Connecticut EEB Botany Award, American Philosophical Society: Lewis and Clark Fellowship) and to J.G.M. (NSF DEB-1557086).

AUTHORS' CONTRIBUTIONS

V.R.M., D.D., J.G.M. and R.B. developed the ideas and prepared the figures; V.R.M. drafted and coordinated manuscript preparation and D.D., J.G.M. and R.B. contributed sections and revisions.

DATA AVAILABILITY STATEMENT

No new data were generated for this review. R code used to produce Figure 5 is publicly available on GitHub <https://doi.org/10.5281/zenodo.3625311> (Milici, Dalui, Mickley, & Bagchi, 2020).

ORCID

Valerie R. Milici  <https://orcid.org/0000-0003-2710-6545>

James G. Mickley  <https://orcid.org/0000-0002-5988-5275>

Robert Bagchi  <https://orcid.org/0000-0003-4035-4105>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Milici VR, Dalui D, Mickley JG, Bagchi R. Responses of plant–pathogen interactions to precipitation: Implications for tropical tree richness in a changing world. *J Ecol*. 2020;108:1800–1809. <https://doi.org/10.1111/1365-2745.13373>