

Review

Tree Diseases as a Cause and Consequence of Interacting Forest Disturbances

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Abstract: The disease triangle is a basic and highly flexible tool used extensively in forest pathology. By linking host, pathogen, and environmental factors, the model provides etiological insights into disease emergence. Landscape ecology, as a field, focuses on spatially heterogeneous environments and is most often employed to understand the dynamics of relatively large areas such as those including multiple ecosystems (a landscape) or regions (multiple landscapes). Landscape ecology is increasingly focused on the role of co-occurring, overlapping, or interacting disturbances in shaping spatial heterogeneity as well as understanding how disturbance interactions mediate ecological impacts. Forest diseases can result in severe landscape-level mortality which could influence a range of other landscape-level disturbances including fire, wind impacts, and land use among others. However, apart from a few important exceptions, these disturbance-disease interactions are not well studied. We unite aspects of forest pathology with landscape ecology by applying the disease-triangle approach from the perspective of a spatially heterogeneous environment. At the landscape-scale, disturbances such as fire, insect outbreak, wind, and other events can be components of the environmental ‘arm’ of the disease triangle, meaning that a rich base of forest pathology can be leveraged to understand how disturbances are likely to impact diseases. Reciprocal interactions between disease and disturbance are poorly studied but landscape ecology has developed tools that can identify how they affect the dynamics of ecosystems and landscapes.

Keywords: forest pathogens; disease triangle; landscape ecology; disturbance interactions; fire; insect outbreak

1. Introduction

Forest diseases occur in an intricate environmental context that is a reflection of long host lifespan and fixed location. In contrast to other foci of disease ecology, environmental influences on forest health have been recognized as important factors influencing disease in individual trees since the emergence of forest pathology as a topic of scientific inquiry [1]. Environmental factors act on pathogens and tree hosts independently and, as a consequence, disease incidence may increase or decrease due to environmental variability. This environmental variation can include year-to-year climate variation (temperature, precipitation, humidity), environmental pollutants (ozone, acid deposition), and a range of biophysical or biotic disturbances such as fire, wind, herbivory or insect outbreak [2,3]. A substantial body of research has developed to elucidate environmental influences on both pathogens and their tree hosts, encompassing a diversity of environmental stresses and effects at scales ranging from cellular to landscape [4,5]. Integrating dynamics of both host and pathogen simultaneously with environmental effects on disease remains challenging, and yet is essential to understanding how forest diseases are likely to change in the future [6].

The disease triangle is a scale-free, flexible, and general model that has been used extensively to determine the etiology of many plant diseases and, more recently, zoonotic diseases. The model is a visualization of host, pathogen, and environment in a tripartite dynamic interaction framework that has been especially useful when applied at the individual-to-stand level. However, this application is in some contrast to the scale of the most problematic disease outbreaks which tend to occur across landscapes or regions [7–9].

The field of landscape ecology focuses on identifying mechanistic processes that lead to landscape-level patterns and the implications of cross-scale interactions in driving these patterns. Scale mismatch among mechanisms that underlie an emergent condition—including disease—is not a problem unique to forest pathology. Landscape ecology has developed understanding of the causes, consequences, and patterns of ecological changes that occur over large spatial scales such as plant community shifts resulting from fire, biotic agents including insects and disease, or land-use patterns [10–12]. Landscape ecology applies to a range of spatial extents, but is often employed to understand changes in collections of heterogeneous ecosystems (a landscape) or regions (a collection of landscapes). The field has developed a range of spatial analysis tools that pair with remote sensing technologies; these efforts have improved understanding of the causes and consequences of spatial patterns as well as increasingly accurate resource inventories.

Forest health researchers have applied landscape ecology approaches to gain insight into disease drivers acting at the spatial extent of a landscape or region [13,14]. These efforts have produced maps of spatiotemporal patterns of disease risk with great management application [10,15]. These advances are also important in that they apply epidemiological theory to large spatial extents although, at the landscape extent, forest pathology has tended to examine disease in isolation from other dynamics and processes. At the same time, understanding ecological dynamics at landscape-to-regional scales is increasingly focused on the role of interactions among disturbances which alter spatial structure and variation [16,17]. We suggest that this is a potential nexus of the two fields that can improve understanding of landscape dynamics as well as the mechanistic basis of disease emergence at broad spatial extents.

Disease forecasting and prediction of the resulting ecological impacts have obvious value to managers and policy makers. Shaping landscape-level structure, such as fuel levels, age-class, or species distribution, demands substantial economic investments. Disturbance events, including but not limited to disease, can challenge these goals and incur great ecological or management costs. Increasing interest within landscape ecology has focused on the overlap and potential interactions of landscape-level disturbances. Global environmental change, including altered fire regimes, changes in regional climate and weather, as well as increased introduction of exotic organisms, are all potential drivers of disturbance interactions that could increase the ecological impacts of these events [16–18]. Landscape-scale models and empirical studies of disease impacts are relatively infrequent compared to fire and land use [16–18]. At the same time, cellular-to-population level studies of disease illustrate considerable variation in intensity and underlying causes that emerge from the components and interactions encompassing the disease triangle. These insights can be leveraged into predictive epidemiological models that account for host susceptibility and transmission, characteristics that are distinct biologically from risk or contagion as applied in models of fire or land-use change. Put another way, disease is an emergent phenomenon with inherent mechanistic differences from other landscape-scale disturbances. Yet diseases are likely to affect, and be affected by, other landscape-level disturbances in ecologically important ways.

This paper examines linkages between forest diseases and landscape-scale disturbances to understand how these distinct events may interact to affect each other. Landscape ecology and forest pathology are notable for strong research foundations that suggest disease–disturbance interactions are likely to shape ecosystems. Yet, very few empirical examples of these interactions have been undertaken in spite of a strong emphasis within both fields on the role of environmental factors. This suggests potential for improving prediction of disease and disturbance impacts through an assessment of

the strengths and research needs in each field. Although pathogens and insects have important differences in how they affect tree health, we examine inferences gained through the study of insect outbreak–disturbance interactions to frame hypotheses of disease–disturbance dynamics from ecosystem-to-landscape scales. Empirical research linking epidemiological process and ecosystem or landscape-level impacts of forest disease is generally lacking, so we also point to several studies aimed at addressing this knowledge gap. Landscape ecology has built metrics for quantifying landscape pattern, processing of remotely sensed data, and models of disturbance dynamics that can be placed within traditional forest pathology approaches. This structure provides a basis for rapid integration of ecosystem-to-landscape impacts and dynamics of disease into landscape models and associated theory. We link these bodies of knowledge by identifying mechanisms of interaction that are likely to determine if or when disease–disturbance interactions are ecologically important.

2. The Disease Triangle: A Primer for Landscape Ecologists

The disease triangle (Figure 1) is a valuable heuristic tool for envisioning and testing drivers of disease emergence. The model has a long history both within forest pathology and plant pathology more broadly [1]. The model frames disease as an emergent condition resulting from interactions of a pathogen with a susceptible host in suitable environmental conditions. Changes to any of the components can accelerate or dampen disease dynamics, while also altering the other components of the triangle. As a general, parsimonious, and dynamic conceptual model, the disease triangle also requires a researcher or manager to contextualize the disease system, including any unique characteristics of the focal host or pathogen.

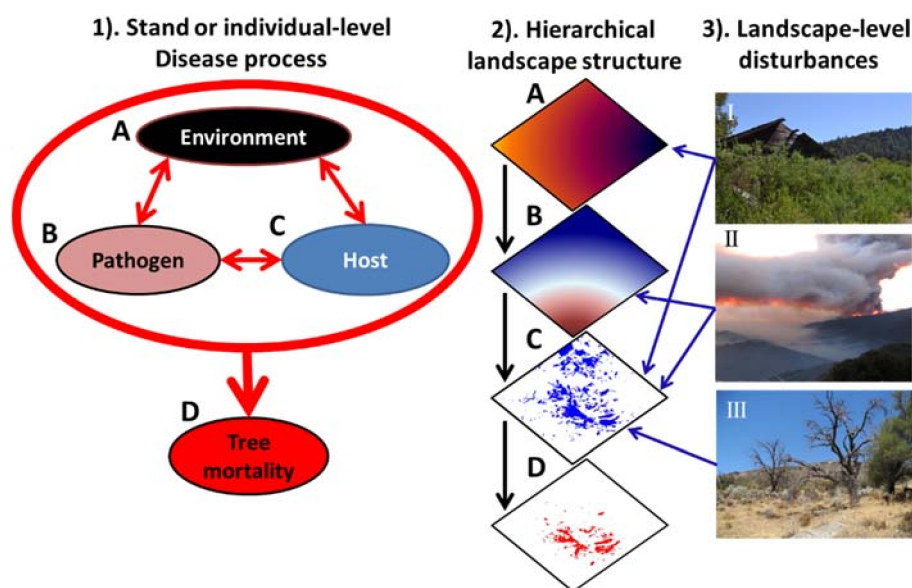


Figure 1. Linkages between forest pathology and landscape ecology with example landscape-level disturbances which can influence disease emergence and impacts. The traditional disease triangle (1) factors (A–C) are shown simultaneously in the spatial context of landscape ecology (2) along with landscape-level disturbances that are likely to interact with disease (3). Environment (1-A and 2-A) is shown on a gradient along with a waveform pathogen invasion process (1-B and 2-B) and realistic spatial heterogeneity of host distribution (1-C and 2-C) and mortality (1-D and 2-D). Examples of interactive disturbances are shown with arrows indicating the components of landscape structure and the disease triangle that are impacted: Invasive plants competitively inhibit forest host reestablishment following land abandonment with impacts to environmental conditions and host distribution (I—*Genista monspessulana* invasion of an old vineyard), fire can alter host and pathogen distribution (II—Soberanes Fire 2016, Big Sur—Photo credit K. Frangioso), and emergent insect outbreak-caused mortality of host populations (III—*Agrilus coxalis* mortality of coast live oak).

2.1. Pathogens

The major disease-causing pathogens of forest trees represent many branches on the tree of life, including fungi, oomycetes, or parasitic plants [3,19]. These pathogens can vary widely in their spatial distribution across a landscape. Some weak or facultative pathogens can be so widespread as to be practically ubiquitous, likely an evolutionary consequence of minimal impacts to host health or primarily saprotrophic energy acquisition [20,21]. Other more aggressive native pathogens such as *Heterobasidion* or *Dothistroma* species may be widespread within a region but only emerge as diseases following land use or climatic changes, respectively [22,23]. In contrast, diseases caused by invasive pathogens are often characterized by introduction foci that strongly control the spatial distribution of disease risk prior to equilibration of the pathogen in a new range. Introduced populations of *Phytophthora ramorum*, *P. cinnamomi*, or the beech bark disease insect-pathogen complex all share this strong signature of spatiotemporal variation in the distribution of disease risk [9,12,24].

2.2. Tree Hosts

Disease emergence or suppression may be driven by shifts in host presence or abundance. In forests, species abundance reflects a range of climate drivers, ecological processes, and cultural practices; several examples of documented or potential increases in disease with changes in host population are worth highlighting in light of these dynamics. Increased cultivation of *Hevea* species for rubber production is implicated in increased frequency and severity of South American leaf blight [19,25], a disease that rarely reaches inoculum levels needed for disease emergence under non-cultivated conditions. Increased tanoak importance in response to inadequate silvicultural investments has also been implicated in patterns of *P. ramorum* establishment risk and emergence of sudden oak death [26–28]. Afforestation in response to changes in land use or fire suppression has also been shown to increase *P. ramorum* hosts and subsequent patterns of disease emergence [29]. Vegetation changes in response to environmental and social or economic dynamics can also shift species abundances and spatial distributions with no significant changes in the represented taxa. For example, in northern forests of Quebec, human impacts reflecting changes in economic factors and silvicultural practices could influence future likelihood of insect outbreak [30]. Plant invasions can also alter host populations at broad spatial scales. In the southern hemisphere, several invasive pine species along with their mycorrhizal symbionts are aggressive invaders of native ecosystems. These invasions cause severe landscape-to-regional scale transformations of forest communities that also transform standing biomass, biogeochemical processes, and biodiversity [31,32].

Hosts also experience changes in susceptibility due to environmental responses at cellular-to-individual scales. Environmentally driven increases in host susceptibility to pathogens are commonly termed host “predisposition” to infection or disease. Tree hosts respond to physical or biotic stresses such as fire, drought, or insect and pathogen attack through a range of physical structures, chemical defenses, and biochemical pathways [4,5]. Thus, the physiological status of individual trees or entire populations can also determine the likelihood of disease emergence.

2.3. Environment

Within the context of the disease triangle, many environmental factors influence disease by limiting hosts or pathogen ranges and through direct influences on pathogens or their hosts. For example, temperature affects pathogen metabolic activity as well as host predisposition in response to environmental stress [33]. Global change-driven range expansions or contractions could make disease emergence more, or less, likely due to changes in the abundance or spatial distribution of either biological component [3,19,34]. Physical host wounds that act as a de facto surmounting of host physical defenses play an important role in infection [1,22,35,36]. Drought has been shown to cause physical damage to plant vascular tissues that may require multiple years to repair [37] and it is likely that other environmental stresses also cause multi-year changes in susceptibility.

Land management can be considered part of the environmental portion of the disease triangle, and is sometimes envisioned as a fourth component. This is warranted as land management policy can be more readily changed compared to an environmental event such as drought; policy and management can also affect environmental drivers of disease or landscape-level host distribution [3,38].

3. The Disease Triangle in the Context of Disturbance

In the absence of disease, disturbances play a critical role in structuring forest communities at local-to-landscape scales [17,30,39]. Ecological disturbances can alter any component of the disease triangle (Figure 1). This creates a dual context for disturbances: they are a component of the environmental portion of the model or also an external factor that can influence host composition or pathogen abundance. These effects in conjunction with environmental changes that determine host stresses or pathogens infection, can also create disturbance-feedbacks that will alter disease dynamics.

3.1. *Environmental vs. Biotic Stress on Tree Hosts*

An intricate system of plant hormone signaling has a strong influence on secondary chemical pathways and allocation of resources to repair physical damage from biotic and abiotic causes. Problematically for plant hosts, biochemical pathways that confer resistance to environmental stress can suppress those that confer resistance to insects and pathogens. The resulting hormonal interference of defensive pathways is known as plant hormonal cross-talk [4] and can be a significant factor leading to increased susceptibility (predisposition). Carbon- or nitrogen-based secondary chemistry can be important factors determining the degree of damage caused by insects or pathogens, but available carbon resources are also important for repairing tissue damage resulting from environmental stresses [5]. This suggests another resource dilemma for trees—whether to respond to environmental stress or biotic attack. Of course, physical damage, heat, and water stress may suppress defensive pathways for biotic attack via hormonal cross-talk [4] suggesting plant response to environmental factors may simply take precedence to biotic attack in some circumstances or species. It is likely that trees are sometimes caught in untenable “catch 22” traps where the host must respond to potentially overwhelming environmental or overwhelming biotic stresses and is likely to be overcome either way.

3.2. *Example Disturbance Effects on Pathogens*

Forest management and fire are especially important disturbances in forested landscapes that have been documented to influence disease dynamics in some circumstances. Each of these events can alter temperature and relative humidity which are particularly important controls on infection success for many important fungal pathogens (Figure 1). Tree harvesting can further alter stand characteristics that influence pathogen dispersal. For example, dwarf mistletoe dispersal is facilitated by increased canopy opening following thinning [40], and it is likely that increased air-flow and reduced tree density also increases the connectivity of susceptible hosts. Harvest and the resulting effects on substrate for pathogen survival, creation of infection pathways, and changes in host distribution or abundance have strong influences on disease emergence [14,20,22]. Increased input of below-ground organic matter, important for inoculum buildup of some root diseases, could occur following a variety of management actions [41,42]. Fire is somewhat unique in that it often causes substantial host and pathogen mortality [43] which should caution researchers against generalization without more examples. In contrast to fire impacts, fire suppression can lead to increased host density, which in turn may increase local inoculum build-up as well as alter microclimate in ways that influence pathogen establishment and the emergence of specific diseases [44].

Non-host plant invasions can also alter mutualistic host–microbial interactions, nutrient availability, and increase competition for other limiting resources such as light and water [45]. Most obviously, strong competitive interactions or competitive exclusion of host species by a novel invader could have powerful influences on disease emergence. However, this kind of shifting species dynamic is more likely when the invading plant amplifies pathogen populations and creates positive

feedback between pathogen and invader [46,47]. Plant invasions can suppress or amplify pathogen populations and the relevance to disease will often depend on the interactions between a specific plant invader and pathogen.

3.3. N Deposition, an Example of Changing Environmental Conditions at Broad Spatial Extents

Environmental contamination has received less attention as environmental drivers of disease, but the spatial scales at which these events occur make them relevant to any discussion of disease–disturbance interactions. Atmospheric N deposition has potential to alter host populations by shifting species composition and dominance via changes in growth rates. N deposition has also been documented to increase pathogen attack [48,49] which may reflect mechanistic drivers from cellular-to-community scales. Studies of N-deposition on disease emergence are more common in understory or herbaceous species but whether this is due to an overall lack of study in overstory trees vs. greater susceptibility in these habitats is unclear. Increased N availability could alter a range of ecological interactions that influence tree host susceptibility such as phyllosphere host–microbial interactions and within-plant carbon allocation [33]. Species invasions, climate change, and other kinds of pollution could alter host or pathogen populations at broad spatial scales and are worth examining for disease–disturbance interactions.

3.4. Disease as Disturbance

Both native and exotic pathogens are substantial ecosystem disturbances that can cause a range of impacts with variable duration and intensities [50]. Root nematode pathogens, aerially dispersed *Phytophthora* pathogens, and native *Phellinus* root pathogens have each been shown to alter biogeochemical processes including nitrogen and carbon cycling [51–53]. Forest structural changes can be dramatic, and include shifts in size class distribution, selective removal of individuals, or changes in species composition [7,12,54,55]. The nature and extent of forest structural changes depend on specific biological characteristics of the pathogen such as the host range and virulence, as well as interactions with the biology of the tree host, including age- or size-related variation in susceptibility or host competency to transmit the pathogen. In the most extreme cases where host range is broad and many hosts suffer disease following infection, pathogens can drive a conversion from one ecosystem type to another. *Phytophthora cinnamomi* is an illustrative example, this pathogen causes the devastating disease Jarrah dieback which can convert woodland or forest to a low-statured heathland [9].

4. Disturbance Interactions: Perspectives from Landscape Ecology

Disturbance interactions are increasingly studied outside of the purview of forest pathology and the associated empirical and theoretical advances are relevant for bridging the fields (Table 1). Landscape ecology has made important advances in framing general theory and expectations regarding how a broad set of disturbances are likely to interact [16,17,56]. These efforts have incorporated differences in frequency, spatial pattern, and severity of physical and biological disturbances with the aim of assessing the relevance to landscape structure and management. Disturbance frequency, patterns, and impacts lie at the core of inquiry in landscape ecology, which stems from the importance of these events in driving spatial patterns [56]. In light of this, it is unsurprising that many of the intellectual frontiers of disturbance interactions (including but not limited to disease) are also firmly rooted within landscape ecology [13,14]. Systems at the landscape spatial scale are so often subject to variation in environmental stresses and stochastic events—such as lightning ignition sources or individual land-use actions—that understanding overlapping disturbances and their interactions is fundamental to mechanistic understanding and prediction over large areas.

Table 1. Example studies linking environmental changes and disease emergence or the interactive effects of biotic agents and landscape-level disturbance dynamics.

Biological Agent	Interacting Disturbance	Comments	Examples
Landscape-level examples			
Native insects	Fire, wind, salvage harvest	Tested for interactive effects	[11,57,58]
Invasive pathogen	Fire	Tested for interactive effects	[18,43,59,60]
Root pathogens	Wind	Focused on environmental drivers of disease	[35,61]
Root pathogens	Management, fire suppression	Etiological investigation of landscape-level disease drivers	[22]
Individual-level examples			
Insects or pathogens	Drought, salt stress, and heat	Synthesis, laboratory experiments	[4]
Pathogens	Drought	Synthesis	[5]

Discrete and intense disturbances—such as insect or disease interactions with fire—are notable for the relative ease of assessing population-level changes to vegetation. In these examples, mortality from either disturbance is rapid and easily recognized. The relative tractability of these study systems further leads to empirical and model based studies [11,56,59]. However, slowly accumulating and large-extent disturbance such as climate change and atmospheric N deposition are much more nuanced and difficult to assess. These events will have strong influences on landscape-level processes including disturbance frequency, extent, and impact but quantifying these dynamics with an empirically-backed and mechanistic framework poses many practical challenges [56].

How landscape scale dynamics affect ecological resiliency is also important for gauging the relevance of disturbance interactions to land management policy. Post-disturbance vegetation recovery rates and successional dynamics have a strong control over ecological resilience to interacting disturbances, for example, by affecting the likelihood of future disturbance events and their intensities [16]. Policy makers and managers face the dilemma that disturbance interactions are known to occur, or are highly likely, yet it is unclear how much these events will challenge local and regional management goals. This problem may be acute when multiple possible successional trajectories emerge from the local species pool and variation in disturbance impacts [17,50]. Despite important uncertainties, enough information is in hand to provide a point-of-departure for quantifying disease–disturbance interactions and incorporating these insights into land management policy.

4.1. Insect–Fire Interactions

Interactions between fire and insect outbreak have received attention among researchers due to the frequent overlap and relative importance of each disturbance [11,57,58]. Although biologically distinct from forest diseases, insect outbreaks provide insights into disturbance interactions and can help formulate expectations given changes to canopy structure, species composition, and changes in biomass distribution. Insect-driven mortality events have been dramatic and cause for alarm among land managers in fire-prone conifer forests of western North America. Many of these forests have been impacted by drought and fire suppression, which have influenced insect population dynamics and host physiological status [62,63]. In this respect, insect outbreaks are a useful model for disease in that tree mortality is driven by environmental changes including climate dynamics and land management. Severe insect-caused mortality often results in a short-term increase in highly flammable canopy fuels followed by an increase in ground fuels as dead material moves from the canopy to the forest floor. Somewhat counter to initial expectations, these mortality patterns have led to an overall decrease in fire impacts as measured by the likelihood of crown-fire, which are often the most damaging and dangerous forest fire conditions, for both bark beetle [11,57] and spruce budworm [58]. In these studies, the timing of fire and insect outbreak events was more important than the spatial overlap of each disturbance.

4.2. Disease–Disturbance Interactions

As previously noted, etiological studies have dominated most applications of the disease-triangle in forest pathology. For example, wind pressure on tree canopies can transfer a substantial amount of tension and compression force to root systems. The resulting wind-caused damage to fine roots is an important pathway of infection and subsequent creation of disease centers in balsam fir-spruce forests of the White Mountains, New Hampshire [61]. Historical management actions including fire suppression and cutting to control bark beetle outbreak have been demonstrated to influence patterns of *Heterobasidion* root disease centers in Yosemite Valley, California [22]. Historical patterns of conifer harvest have also likely influenced the landscape-level distribution of invasion risk for *P. ramorum* in coastal California and Oregon [24]. However, for each of these example systems, there has been little effort to inform prediction of future resource status, disturbance patterns, and rates (or capacity) of ecosystem recovery [17,56]. For example, wind-driven root infection decreases tree capacity to withstand wind events. Thus, wind can facilitate disease which then renders stands or ecosystems more vulnerable to wind-driven mortality [61]. Problematically, temporally delayed disease–disturbance interactions could be easily masked and result in misattribution of underlying mortality causes [50].

The few published studies focused on disease–disturbance interactions provide some insights that may help overcome this research challenge. The authors of this article along with colleagues conducted a series of studies examining interactive impacts of *P. ramorum* and fire in coastal California forests. Using a set of permanent study plots in disease-impacted forests that were surveyed before and after the 2008 Basin Fire, this work showed that fire impacts are contingent on the stages of disease progression, supporting comparisons to insect–fire interactions (compare with [57]). In our plots, fire intensity was positively related to the amount of fine canopy fuels associated with recently killed trees and decreased as these materials move from the canopy to the soil surface [18]. In contrast, fire-caused mortality of redwood, a species that is resilient to *P. ramorum* and typically also resilient to fire, increased with greater accumulation of ground fuels [59]. This pattern suggested that disease-generated fuels accumulated to the point that damage to tree root systems or cambium tissue was substantially increased. Ground fuel accumulation also impacted soil resources, losses of critical soil nutrients and carbon increased with increasing disease-related mortality [60], changes that may in turn alter post-fire vegetation succession. Although these studies are associated with an individual disease and fire (i.e., a single example), the mechanistic link between mortality, fuels, and ecosystem impacts suggests these disease–disturbance interactions could occur where other disease and fire events overlap.

5. Frontiers in the Study of Disease–Disturbance Interactions

Approaching a new study system or challenge with the most parsimonious model is often a recipe for rapid advancement. With some notable exceptions [11,17,56], most interactive disturbance studies have focused on two events. In the sudden oak death system, our sole explicit test of disease–disturbance interactions, we studied a single forest disease and a single fire. This study system spans multiple forest types which provides insight into variation in disease impacts, the importance of pre-disease species composition and structure [18,43,59,60] but ultimately provides only a partial view on the importance of interactive impacts. For example, our Big Sur study region is a fire-prone landscape that burned with a landscape-level wildfire only eight years following our initial study (the 2016 Soberanes Fire). How do repeated or subsequent disturbances modify or reflect previous disease–disturbance interactions? In the case of Big Sur and sudden oak death, *P. ramorum* was found to rapidly reinvade following the initial 2008 Basin wildfire [43], presumably impacts from the recent 2016 Soberanes wildfire reflect both the previously documented disease–fire interactions as well as an additional eight years of disease that occurred between wildfires. In Yosemite Valley, *Heterobasidion* disease centers are a serious public safety concern as several deaths have been associated with failures of infected trees [22]. This has motivated the aggressive removal of at risk trees, particularly in high-recreation use areas, as well as the greater application of prescribed burning in other parts of the valley. Yet, it is unclear how these management actions have influenced disease dynamics and

furthered public safety beyond the immediate danger of tree failures. In both cases, disease–disturbance interactions could be reasonably argued to have increased or decreased ecological impacts under specific edaphic, vegetation, or management conditions.

Third and fourth-order disease–disturbance interactions remain minimally studied although these are certain to represent future management challenges. Fire-prone regions where multiple fires and disease events occur over time could be shaped by these factors. Paine et al. [56] and Johnstone et al. [17] suggested several general ecosystem trajectories resulting from disturbance interactions that tend to focus on transitions between stable ecosystem states or temporary states associated with recovery (Figure 2; examples 1 and 2). We recognize that these expectations may also fit disease–disturbance interactions. For example, disease-center formation in the White Mountains of New Hampshire resulting from wind impacts is a temporary ecosystem state [35,61]. Similarly, it has not yet been shown that sudden oak death–fire interactions will lead to long-term and permanent shifts in forest structure although it is plausible that increased tree mortality and soil nutrient loss will result in these changes. However, biotic disturbances are strongly influenced by the coincidence of environmental conditions favorable to establishment or outbreak suggesting that dynamic ecosystems should be expected in some circumstances (Figure 2; example 3). Oscillating dynamics where host populations recover and provide the basis for future outbreaks are a common pattern in many tree mortality events driven by native organisms [35,51,62]. Intensifying outbreaks resulting from climate-change-associated shifts in temperature, precipitation, and resulting host-stress appears likely given documentation of landscape-level declines in host physiological status and its impact to plant defense [3,4,37].

Hysteresis is a common challenge for much of ecology and the importance as well as the difficulty of capturing these effects is increased in studies at the landscape scale. The difficulty of scaling-up of results from the plot or stand scale where most ecological inquiry is made to the landscape scale is a common challenge in landscape ecology including the study of interactive disturbances [14,16]. An especially complex factor is that as the landscape is changed, the dynamics within the unit of study may become more dependent on processes and structure external to the measurement unit, often the plot or stand (see Meentemeyer et al. [14]). These changes may require many years to emerge as well as quantify, suggesting that surprises, often problematic to management goals, are likely to emerge without the tools to make judicious forecasts of disease–disturbance impacts. Several lines of inquiry can help prevent these problems: (1) increased efforts to disentangle three-way interactions that lead to disease at broad spatial scales. Disease-triangle applications are biased towards etiological descriptions of disease, yet disease emergence could be a secondary or contributing factor influencing tree mortality and disturbance interactions [19,37]. Understanding if disease is a cause (primary agent) or a symptom (secondary agent) of a forest health problem is essential to any response. (2) Increase focus on multi-pathogen systems. Tree mortality from one event, such as the invasion of an exotic pathogen is likely to alter the conditions for the emergence of a second pathogen. For example, native *Armillaria* pathogens are widespread in forests at risk to *P. ramorum* invasion and the substantial addition of buried coarse roots is likely to increase local *Armillaria* biomass and associated disease [8,20]. (3) Increase the scope of disease–disturbance studies to pathogens with different epidemiological dynamics, plant parts which are attacked, and impacts to host health. At present, studies of fire–insect outbreak has examined insects which attack both the bole as well as the canopy of hosts [57,58]. A broad range of pathogens attack roots and leaves which may alter the timing and duration of dead fine fuels in the canopy; previous work has shown this to be a critical factor influencing disease–fire relationships [18]. Contrasting these classes of pathogens with bole-canker pathogens, vascular wilts, and a range of other biological differences among pathogens [5] could help link pathogenicity with effects on other disturbances.

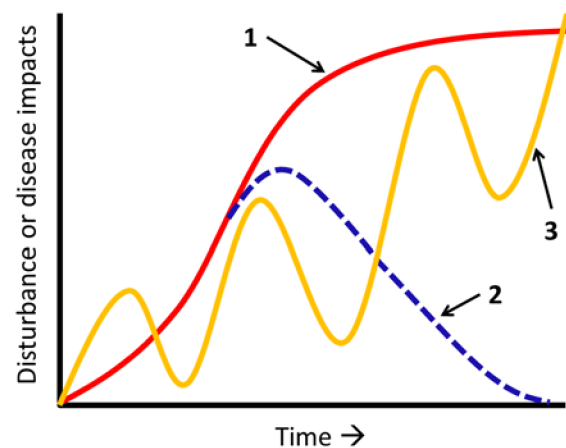


Figure 2. Several examples of disturbance and disease interactive outcomes over time. Impacts may increase and reach a new stable state (1—red); increases may gradually recover to pre-outbreak levels (2—blue dashed); or feedbacks between disease and disturbance could create fluctuating dynamics over time, here depicted as an oscillating, but increasing impact (3—yellow).

6. Conclusions

Landscape-scale disturbances such as wind, fire, or land use can (i) modify the impacts of a disease [22,61]; or (ii) can be influenced by disease in a manner which increases or decreases the ecological impacts of these disturbances [59]. In both cases, the potential to magnify the ecological impacts of either disturbance can have important management implications [16,17], but the mechanistic processes driving these impacts are quite different. The disease triangle is a valuable model for improving understanding of disease–disturbance interactions but to date, the approach has been primarily employed to study environmental influences on disease emergence. This body of work provides the mechanistic foundation for landscape ecologists to model disease emergence at broad spatial scales along with providing the basis to address associated management goals and challenges. However, the influence of disease on other disturbance processes is less well studied, and although the disease triangle is fully reciprocal, little effort has focused on disturbance changes stemming from ecosystem-to-landscape level impacts of disease. A nexus of interest and research efforts is developing between the fields [13,14]; forest pathology can provide epidemiological foundations unique to understanding disease emergence while landscape ecology can provide broad spatial extent models and empirical assessment of ecosystem and landscape dynamics. Of course, more data on ecological impacts of disease and collaboration between forest pathologists and landscape ecologists is needed to develop and test predictions of disease–disturbance interactions that will inform management decisions. However, each field is primed to take advantage of knowledge gained from the other and determine when, if, or how disease–disturbance interactions can be incorporated into land management policy and actions.

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